
POLLINATION AND THE EVOLUTION OF BREEDING SYSTEMS IN PANDANACEAE¹

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ABSTRACT

The Pandanaceae include three genera: *Pandanus* with 700 species and a large range, *Freycinetia* with 200 species and a smaller range, and *Sararanga* with two species and a very limited range. Using Cyclanthaceae, Araceae, and Arecaceae as outgroups, cladistic analysis of Pandanaceae suggests *Pandanus* and *Sararanga* to be more closely related to each other than either is to *Freycinetia*. Data concerning pollination biology and breeding systems are superimposed upon the consensus tree derived from this analysis. Vertebrate pollination and dioecism appear to be ancestral in Pandanaceae, with anemophily in *Pandanus* and entomophily in *Sararanga* to be independently derived conditions. Only a few changes in inflorescence morphology were necessary to facilitate these profound changes in pollination syndromes. Dioecism, while perhaps adaptive for vertebrate-pollinated Pandanaceae such as *Freycinetia*, may have been maladaptive for *Pandanus* and *Sararanga*. The ill-effects of dioecism on long-distance dispersal have been partially overcome in *Freycinetia* by the evolution of "leaky dioecy" and self-compatibility and largely overcome in *Pandanus* through the evolution of facultative apomixis. The deleterious effects of dioecism appear to be unmitigated in *Sararanga* and may lead to its eventual extinction. The interplay of pollination syndromes and breeding systems appears to have strongly influenced range expansion and speciation in the Pandanaceae.

Within the last decade or so, great interest has been directed toward the evolution of breeding systems in seed plants, particularly the evolution of different sexual systems such as monoecism, dioecism, and gynodioecism. Traditionally these systems have been considered to be disparate and distinct, providing the basis for various classification schemes such as the sexual system described by Linnaeus (Linnaeus, 1754). However, by considering a plant to be a metapopulation of modules (White, 1979), the recognition of nested modular levels in plants permits analysis of the different sexual systems at the modular level. Using this modular approach, all sexual systems can be considered merely as combinations of monomorphic or dimorphic sexual strategies (Cox, 1988) at different modular levels. Thus, for example, monoecism and dioecism can both be considered asexually dimorphic strategies occurring at the level of the shoot and the individual, respectively. Using the techniques of evolutionary game theory (Maynard Smith, 1982) as developed for sex allocation theory (Charnov, 1982) these different sexual strategies can be examined for evolutionary stability in any particular population. By definition,

an evolutionary stable strategy (ESS) is one such that if all members of a population adopted it, then no individual with a different strategy could invade the population through the forces of natural selection (Maynard Smith, 1982).

The strength of the combination of game theory and a modular approach is that the effects of various ecological factors on the evolutionary stability of different breeding systems can be examined quantitatively. For example, vertebrate pollination was found to maintain dioecism as the evolutionarily stable breeding system in *Freycinetia reineckei* in Samoa (Cox, 1982). However, a weakness of this approach, and indeed one shared by all ecological approaches to evolution, is that ecological plausibility does not necessarily imply evolutionary causality.

The questions of real interest in evolutionary ecology do not merely address the factors that currently maintain a particular trait (such as dioecism), but rather seek the factors that favored the evolution of the trait. However, such determinations cannot be made effectively by an ecological analysis without due consideration of the phylogenetic relationships involved. Indeed, ecological

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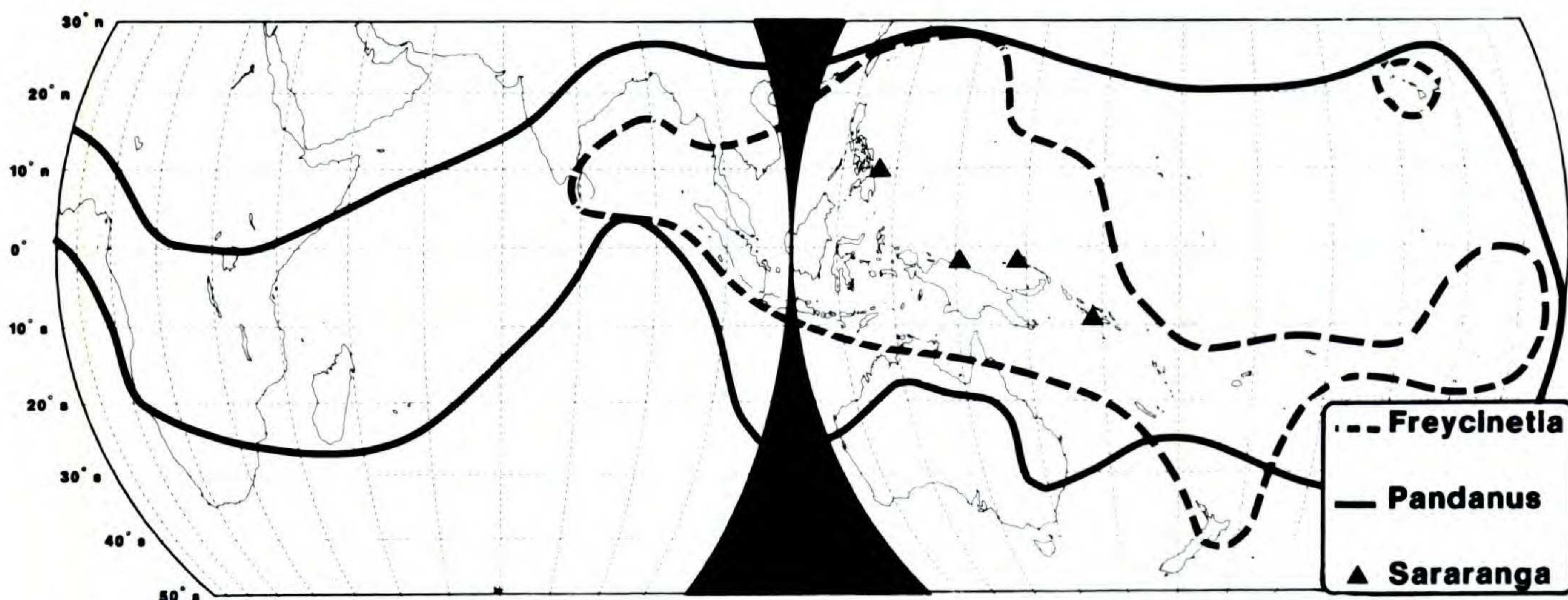


FIGURE 1. Geographical distribution of the Pandanaceae.

approaches to evolutionary questions may produce serious errors in interpretation if phylogenies are ignored.

For example, an ecological analysis of the childhood diseases of nineteenth- and twentieth-century European royalty, using the incidence of disease in commoners as a control, would indicate a significant correlation between hemophilia and access to silver drinking vessels, perhaps suggesting silver to be a causal factor in hemophilia. However, this "silver chalice fallacy" can be avoided by examining the genealogy of the group, which clearly indicates that hemophilia among European royalty is inherited from a single autosomal mutation in Queen Victoria.

Cognizance of phylogenetic constraints can also give an indication of characters that are unlikely to have evolved in a particular lineage. Androdioecism is very unlikely to have evolved in any of the ancestors of, for example, *Scaevola taccada* (Goodeniaceae), since phylogenetic analysis shows that all of *Scaevola* and indeed nearly all of the Goodeniaceae have anthers that dehisce and wither in bud, with pollen being presented by the pendulous, indusiate stigma. Thus, it would be very difficult for a male to disperse its pollen in the absence of a morphologically complete gynoeceum.

Therefore when examining breeding system evolution in the Pandanaceae, to avoid some of the pitfalls inherent in plausibility arguments based solely on ecological considerations, it is advantageous to determine first the phylogenetic history of the group. Once a phylogenetic hypothesis, in this case represented as a cladogram, is determined with some degree of confidence, various trends of evolution of the breeding system within the group can be analyzed within this systematic context. Note, though, that the resultant analysis should be

considered only as a hypothesis, since its validity ultimately rests upon the putative phylogeny, which may change as more information becomes available.

SYSTEMATIC RELATIONSHIPS IN PANDANACEAE

The Pandanaceae, the sole representatives of the Pandanales, are arboreous or scandent monocotyledons confined to the Old World tropics and subtropics (Fig. 1). The family consists of three genera. *Pandanus* is made up of approximately 700 species of trees ranging from the Society Islands to west Africa on an east-west axis and from Australia to the foothills of the Himalayas on a north-south axis (St. John, 1965; Stone, 1976b). *Freycinetia* is a genus of about 180–200 species of lianas ranging from the Society Islands to Sri Lanka on an east-west axis, and from New Zealand to the Himalayas on a north-south axis. *Sararanga* comprises two arboreous species: *S. philippinensis* from the Philippines, of which few recent collections exist; and *S. sinuosa*, which is found along the edge of the Tethys geosyncline in the Solomons, Admiralties, and North Irian Jaya.

The Pandanaceae are very distinctive and disjunct monocotyledons and likely are a group of great antiquity: *Pandanus* pollen has been described from the late Cretaceous and early Tertiary (Jarzen, 1978; Muller, 1981) while at least one megafossil from the early Eocene has been attributed to the family (Nambudiri & Tidwell, 1978; Bande & Awarthi, 1986).

Systematic studies of the Pandanaceae have been made by several investigators including Warburg (1900), Martelli (1934), Merrill & Perry (1939), and most recently St. John (1960, and elsewhere),

Stone (1968a, and elsewhere), and Huynh (1980). The revision of *Pandanus* by St. John (1960, and elsewhere) is now in its 47th part, and the monograph of *Freycinetia* by Stone (1967, and elsewhere) will soon be completed. However, even though Pandanaceae appear to represent a monophyletic group, the relationship of Pandanaceae to other families of monocotyledons remains poorly understood. Conjecture regarding the systematic relationships of the family ranges from the view that Pandanaceae are very primitive monocotyledons to the view that they are very advanced. Meeuse (1965, 1966) suggested the Pandanaceae are relict representatives of the fossil order Pentoxylales, while Engler & Gilg (1924) regarded it as the most primitive monocotyledonous family with affinities to the Typhales (a view shared by Rendle, 1904, and Takhtajan, 1980). However, Stone (1972a) and Cronquist (1968) suggested affinities with Araceae and Cyclanthaceae, a view which has been supported recently through phenetic analysis by Dahlgren & Clifford (1982) and in a cladistic revision by Dahlgren & Rasmussen (1983). However, the precise relationship of Pandanaceae to other families of monocotyledons remains undetermined as even its sister group has yet to be demonstrated convincingly.

Relationships among the genera of Pandanaceae are similarly unclear even though these three genera are quite distinct; as Stone (1972a) pointed out, there are no "freycinetoid" *Pandanus* species and no "pandanoid" *Freycinetia* species. Stone suggested that *Freycinetia* is the most "specialized" genus but "somewhat more distant from the other two genera than the latter two are from each other" (Stone, 1972a, p. 40). Stone believed *Sararanga* possesses the greatest number of primitive characters. In a similar vein, Dahlgren et al. (1985) argued that "*Sararanga* is more ancestral in its floral construction than either of the other genera."

Stone's (1972a, 1982a) view of the relationships among the three genera, with *Sararanga* and *Pandanus* being more closely related to each other than either is to *Freycinetia*, is supported by my preliminary cladistic analysis of generic relationships within the family. Three major difficulties were encountered in this analysis at the generic level. First and foremost among these is lack of a clear sister group to Pandanaceae, although Araceae, Arecaceae, or Cyclanthaceae are all potential outgroups (Harling, 1958; Dahlgren & Clifford, 1982; Dahlgren & Rasmussen, 1983; Dahlgren et al., 1985). Second, the taxonomic status of these potential outgroups is unclear. If, for example, the Cyclanthaceae prove not to be monophyletic, their

use as a single outgroup in a cladistic analysis would be invalid. Third, the distinctiveness of the family makes it difficult to find a large number of characters that vary at the generic level within the Pandanaceae but remain constant at the familial level in the outgroups. This would not be a problem if in-group analysis had been done within these other families, but such analyses are far beyond the scope of this paper.

To overcome these problems, the potential outgroups Araceae, Arecaceae, and Cyclanthaceae were represented by single genera. These genera—*Rhaphidophora* (Araceae), *Balaka* (Arecaceae), and *Asplundia* (Cyclanthaceae)—were chosen solely on the basis of my familiarity with them in the field, although in the case of *Asplundia* my observations were checked against Harling's (1958) monograph of the Cyclanthaceae. Fourteen different character states were scored for these outgroup genera and the three genera of the Pandanaceae. Using this data matrix (Table 1), the most parsimonious cladogram for the Pandanaceae was determined for each outgroup. All three of these trees, however, were found to have the same general topology (Figs. 2–4), which indicates that *Pandanus* and *Sararanga* are more closely related to each other than either is to *Freycinetia*. This result is believed to be relatively robust since the general topology remains unchanged even when the entire Cyclanthaceae, Araceae, and Arecaceae are used instead of their representative genera as outgroups, although the character number is reduced. From these three different phylogenetic trees, a consensus tree (Fig. 5) can be drawn that shows features common to the other trees. As a caveat it should be noted, however, that despite the tremendous efforts of workers such as Stone and St. John, Pandanaceae in general remain poorly collected and insufficiently studied, and hence this preliminary analysis of generic relationships is subject to revision as data accumulate. Monophyly of the genera, for example, should be rigorously demonstrated rather than assumed as I have done here. The current analysis is intended as a method of generating hypotheses concerning evolution of plant breeding systems and as a means of pointing out areas where more information is required.

In the consensus tree (Fig. 5) Pandanaceae are characterized by three synapomorphies, namely spiny leaf margins, dioecism, and tristichous phyllotaxy (characters 12, 13, and 14, respectively). A fourth character, clustering of ovaries into syncarps, is a probable synapomorphy for the family but was not used in this analysis since many apparent reversals occur, such as sections *Acrostig-*

TABLE 1. Character states in Pandanaceae.

Num- bers	Character transition (old to new)	<i>Frey- cinetia</i>	<i>Pan- danus</i>	<i>Sara- ranga</i>	<i>Raphi- dophora</i>	<i>As- plundia</i>
1.	Numerous ovules to solitary ovule	0	1	1	0	0
2.	Parietal placentation to other placentation type	0	1	1	1	0
3.	Seeds unprotected by seedcoat to thick, or endo- carp thick	0	1	0	0	0
4.	Spikes arranged in pseudoumbellate involucre to spikes otherwise disposed	1	0	0	0	0
5.	Inflorescence bracts not fleshy to inflorescence fleshy	1	0	0	0	0
6.	Inflorescence spicate to inflorescence paniculate	0	0	1	1	0
7.	Primary phyllotaxis maintained to secondary tor- sion causing pseudospiral leaf arrangement	0	1	1	0	0
8.	Phyllotaxis same in juvenile and adult to phyllo- taxis changes with maturity	0	0	1	0	0
9.	Leaves with sheathing base or auricle to leaves without sheathing base or auricle	0	1	1	0	0
10.	Aerial roots present to aerial roots not present	0	0	1	1	0
11.	Scandent habit to arboreous habit	0	1	1	1	0
12.	No spines on leaf margins to spines on leaf mar- gins	1	1	1	0	0
13.	Breeding system various to breeding system dioe- cious	1	1	1	0	0
14.	Phyllotaxis various to phyllotaxis tristichous	1	1	1	0	0
15.	Tepal primordia present to tepal primordia ab- sent	0	1	1	0	0

ma, *Jeanneretia*, *Bryantia*, *Curviflora*, *Maysops*, and *Cauliflora* of *Pandanus*, which have single-celled drupes that are not connate into phalanges (Stone, 1972b). The belief that these cases illustrate reversals from ancestral forms with compound ovaries must remain an assumption until a cladogram for internal relations of genera and subgenera within Pandanaceae is developed.

Major characters of systematic importance within the family include ovule number (character 1), placentation (character 2), and secondary torsion in the phyllotactic arrangement (character 7). *Pandanus* and *Sararanga* are characterized by solitary ovules, absence of tepal primordia during floral organogenesis, and leaves without sheaths or auricles at the base. However, *Pandanus freycinetioides* and *P. parvus* exhibit rare or occasional multiple ovules (though few—only two or three) (Cheah & Stone, 1975). The evidence for tepal primordia is based on only a few examples out of some 800 species. In *Pandanus* and *Sararanga* juvenile (i.e., prereproductive) axes, the initial tristichous arrangement of the leaves is obscured by secondary torsion of the axis, creating a pseudospiral leaf arrangement (Figs. 13c, 15c). The sister group to *Pandanus* and *Sararanga*, *Freycinetia*, is characterized by numerous ovules, the presence

of tepal primordia during floral organogenesis (Fig. 8b), no secondary torsion in the tristichous phyllotaxis, and auricles at the leaf bases. The systematic usefulness of the last-mentioned character at an intergeneric level may be subject to revision, however, as studies of leaf organogenesis in all three genera of Pandanaceae and in the probable outgroups are necessary to test whether auricles and leaf sheaths have a similar ontogeny and are indeed homologous. Such an ontogenetic analysis is important since the leaf bases in *Pandanus* sect. *Jeanneretia* and sect. *Dauphinensia* have auriclelike sheaths almost as distinct as in *Freycinetia*, though they are not caducous.

Two autapomorphies (characters 4, 5) characterize *Freycinetia* in all three trees: fleshy bracts (Fig. 6c) and telescoping of the inflorescence, which results in a pseudoumbellate involucre. The role of both features in pollination will be discussed later. There is an additional possible autapomorphology, viz. epidermal-cell papillae on filaments of stamens (Stone, 1971).

A single autapomorphology, i.e., seeds protected by a hard endocarp (character 3), characterizes *Pandanus* in the consensus tree.

Sararanga is characterized by a single autapomorphology common in the consensus tree: an onto-

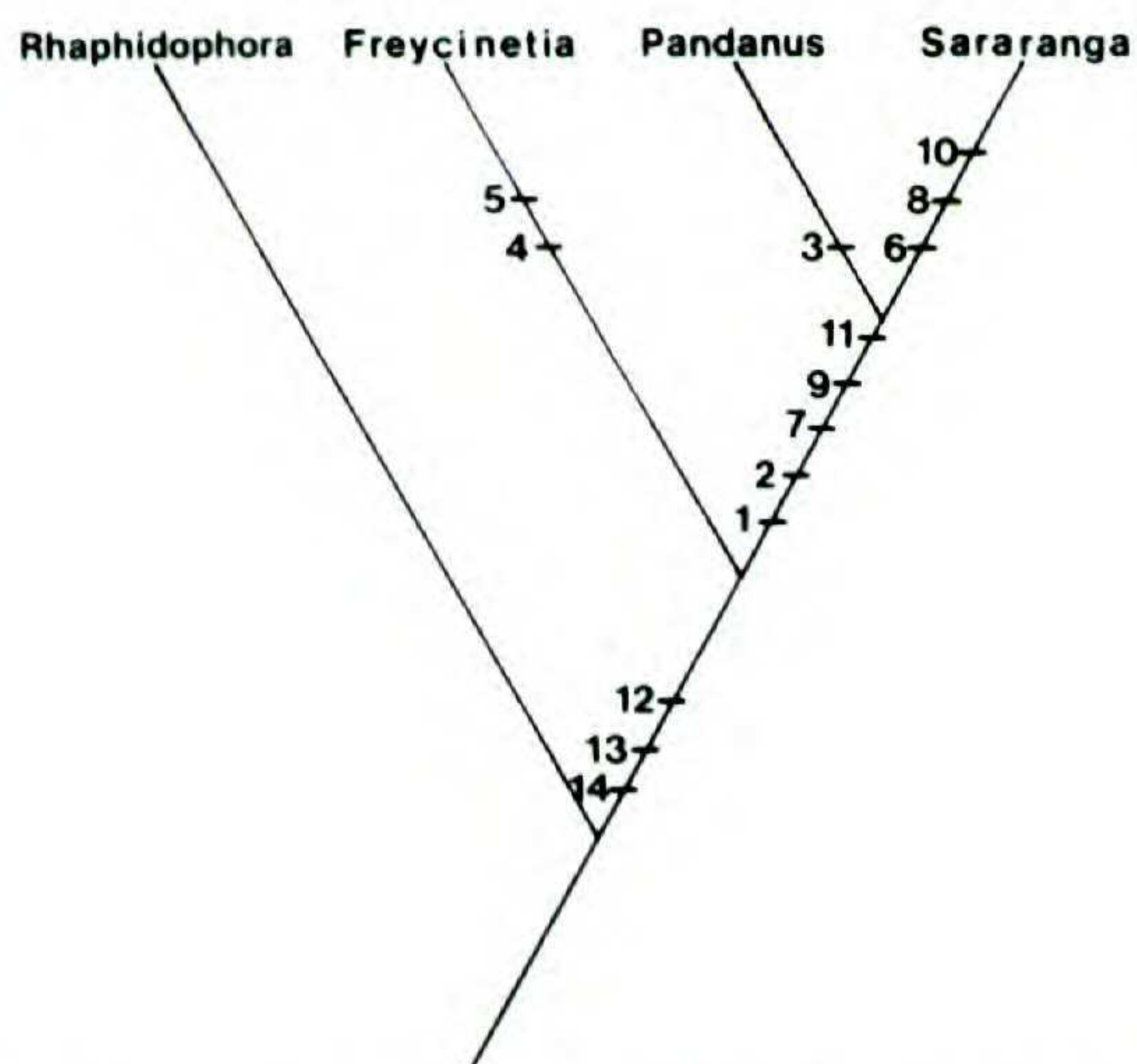


FIGURE 2. Most parsimonious cladogram of the Pandanaceae using the characters in Table 1 and using *Rhaphidophora* (Araceae) as the outgroup.

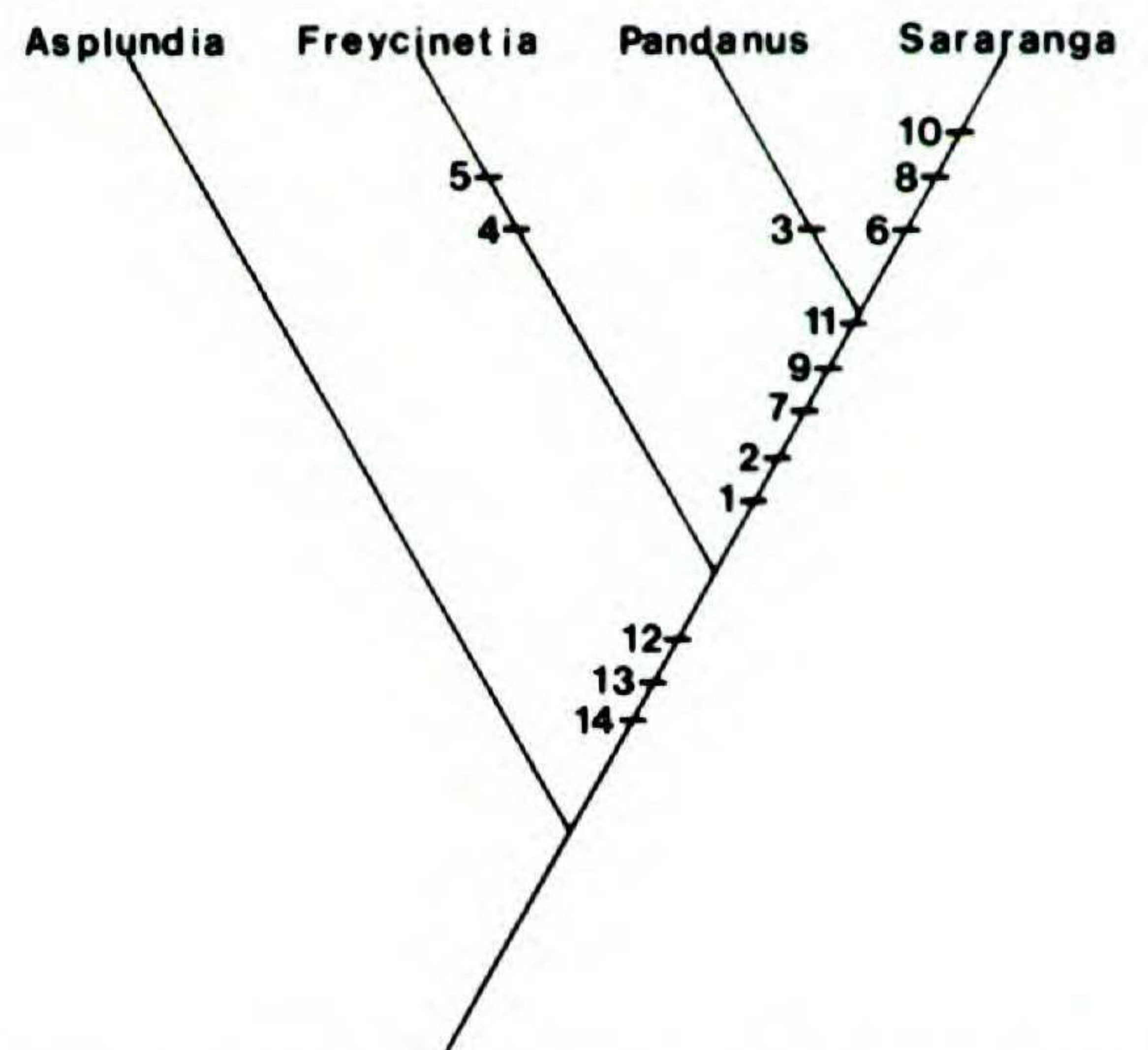


FIGURE 4. Most parsimonious cladogram of the Pandanaceae using the characters in Table 1 and using *Asplundia* (Cyclanthaceae) as the outgroup.

genetic change in phyllotaxis (character 8). Since this change has not previously been noted it merits brief discussion here.

In *Sararanga sinuosa* Hemsl. populations in Guadalcanal (Fig. 7), Tulagi Island (Fig. 8), and along the Siota Passage dividing big and little Ngela islands, I noticed a distinct difference in phyllotaxis in axes produced before and after flowering. The seedling and juvenile axis (Figs. 9, 10, 11) is always tristichous, in this respect resembling the phyllotaxis of *Pandanus* and *Freycinetia* juvenile and adult axes. As this orthotropic axis develops, a secondary torsion results in a pseudospiral leaf arrangement similar to the adult and juvenile axes of *Pandanus*.

The tristichous axis of *Sararanga* continues growth without branching to a height of approximately 6–10 m when it is terminated by an inflorescence (Figs. 7c, 10c, 10d). Three buds in the

axils of leaves beneath this inflorescence continue growth, but these axes and all subsequent axes appear to be tetrastichous, with their leaves in four rather than three ranks, and lack any secondary torsion of the axis (Figs. 10, 11). The precise nature of the phyllotactic arrangement in these secondary axes can be determined by measuring the length of very young leaves using a method developed by Don Kaplan (pers. comm.). For this purpose, buds of primary and secondary axes of *Sararanga sinuosa* Hemsl. collected in Tulagi and Guadalcanal were dissected from the axes in the field and then pickled in FAA (Fig. 11). These buds were subsequently sectioned serially. Each section was examined for the first or last appearances of a leaf. Thus the length of each leaf could be found by multiplying the number of sections it occurs in by the section thickness (in this case 5 μm). This

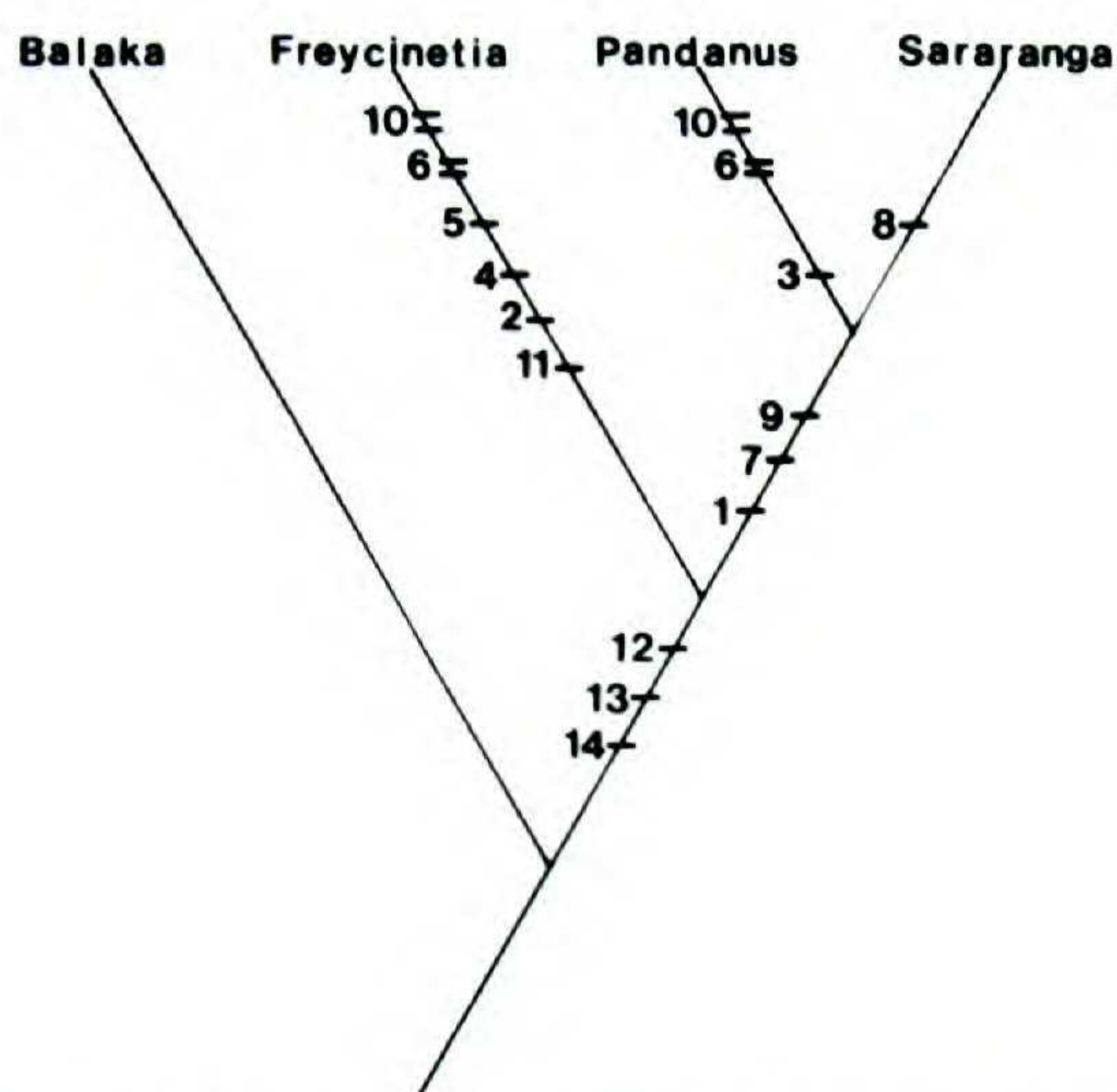


FIGURE 3. Most parsimonious cladogram of the Pandanaceae using the characters in Table 1 and using *Balaka* (Areceaceae) as the outgroup.

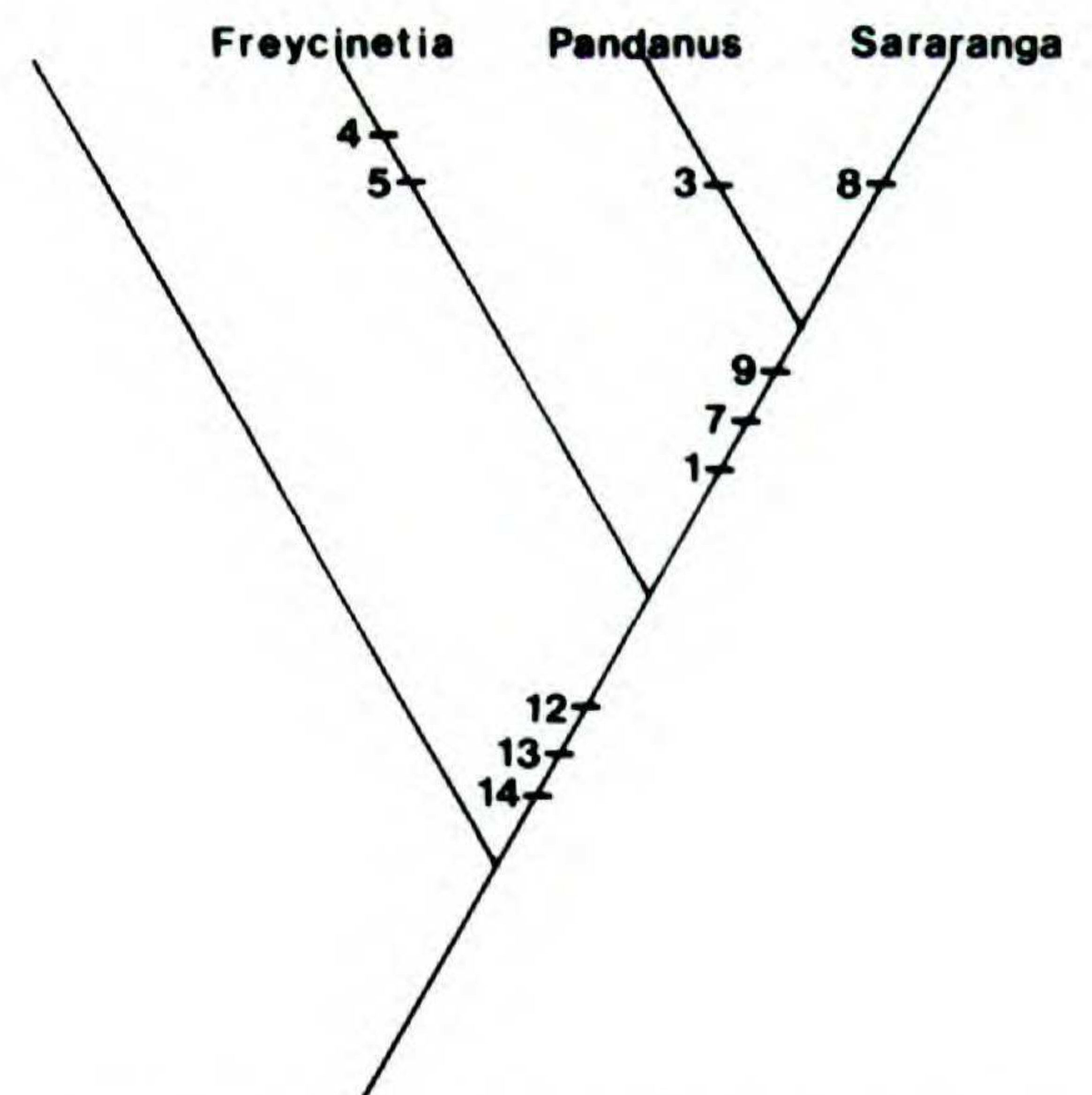


FIGURE 5. Consensus cladogram of the Pandanaceae using cladograms shown in Figures 2–4. Only character polarities common to all three cladograms are shown.

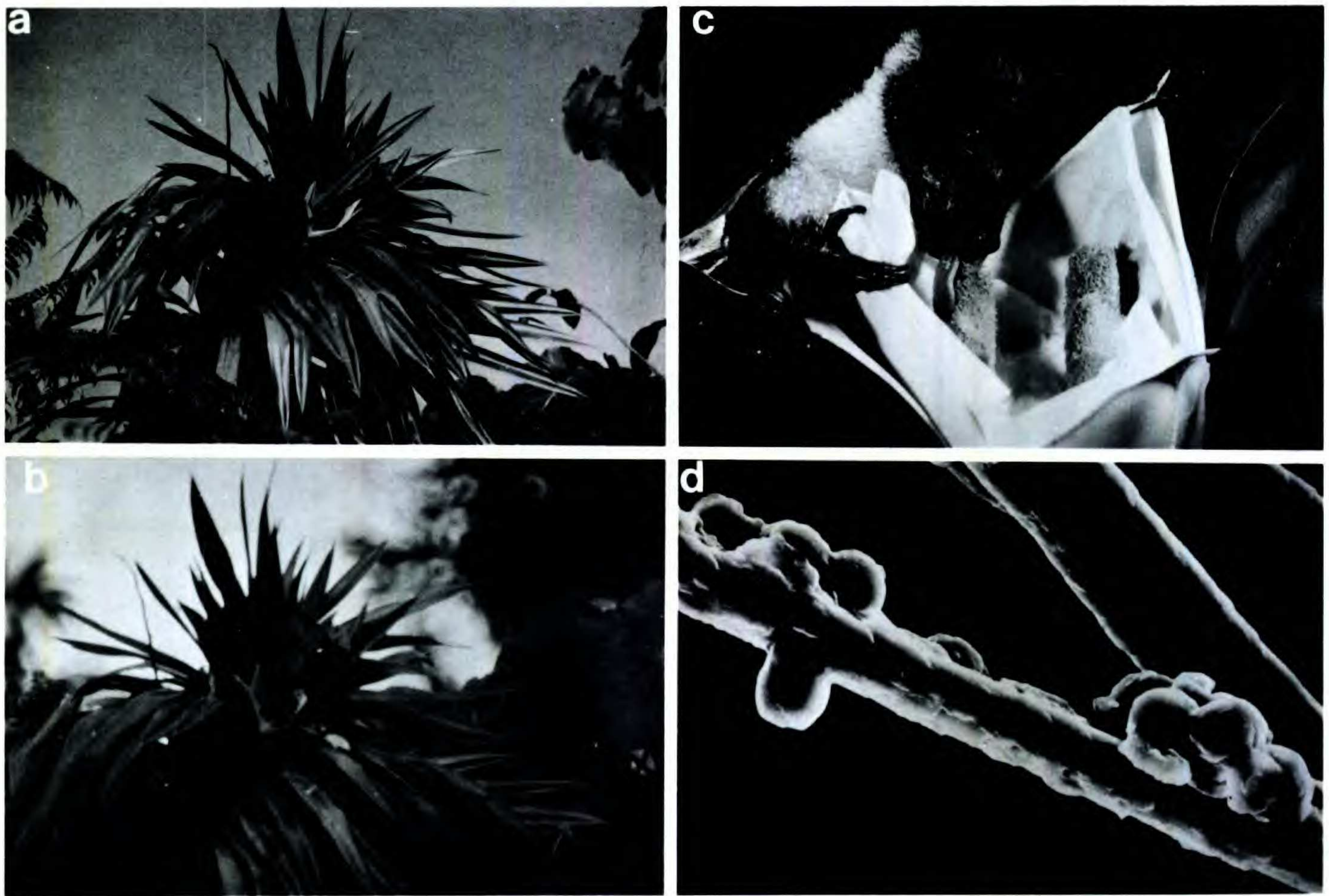


FIGURE 6. Pollination biology of *Freycinetia reineckei*.—a. Habit.—b. Pollination by *Aplonis artifuscus* (Sturnidae) in Samoa.—c. Pollination by *Pteropus marianensis* (Pteropidae) in Guam (photo by Merlin Tuttle, Bat Conservation International).—d. Pollen on facial hairs of *Pteropus samoensis* (Pteropidae) in Samoa. (Figures used with permission from J. Lovett Doust & L. Lovett Doust (editors), *Plant Reproductive Ecology: Strategies and Patterns*. Oxford Univ. Press, Oxford.)

analysis revealed that the apparent tetrastichy of mature (postreproductive) *Sararanga* axes results from a distichous leaf arrangement with each successive node producing a pair of opposite leaves in a plane orthogonal to the plane of the leaf pair produced by the previous node. This arrangement is obscured by the highly compressed internodes except in the inflorescence axis where the internode length is increased, and the distichous phyllotaxis is apparent.

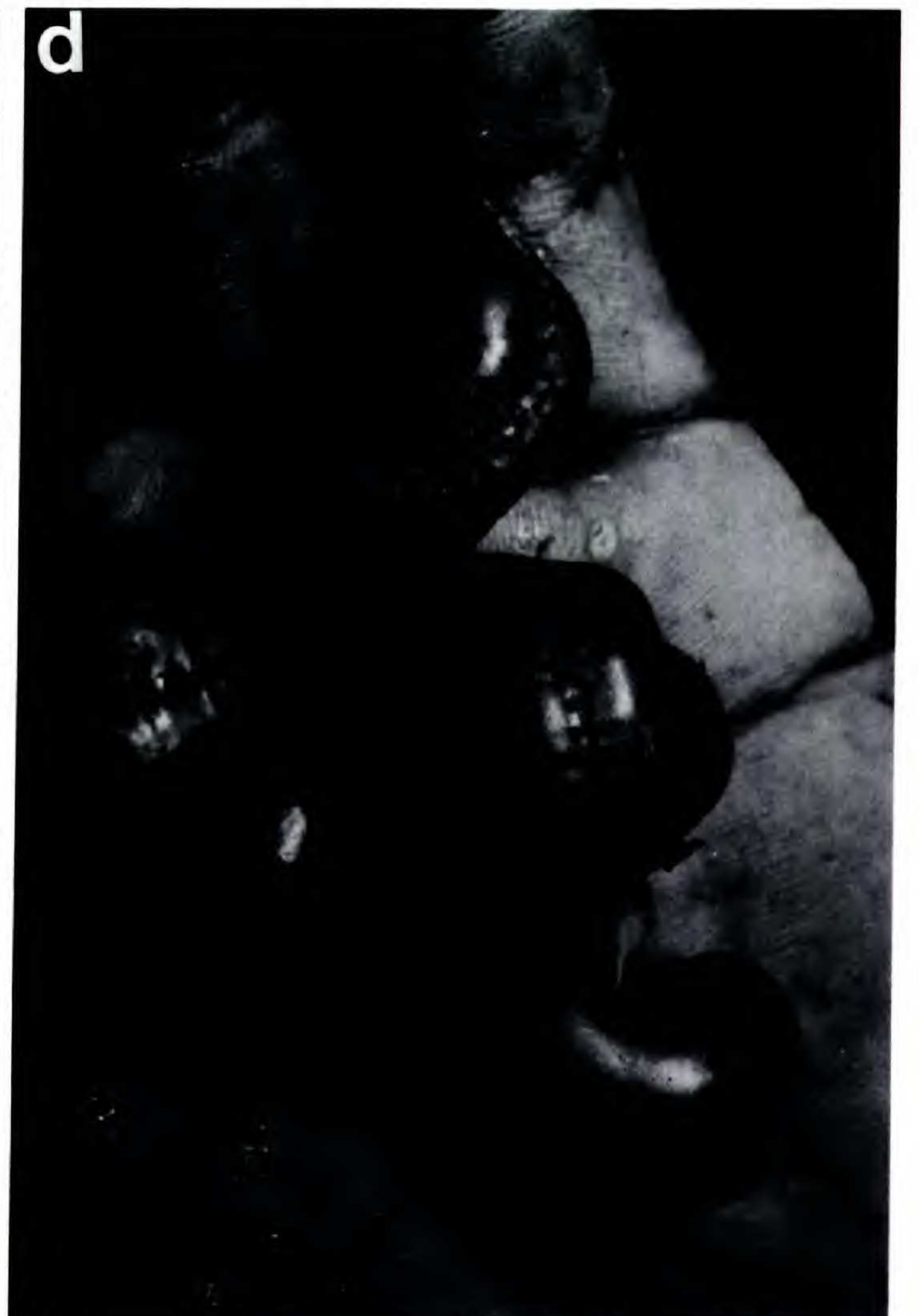
REPRODUCTIVE BIOLOGY IN PANDANACEAE

FREYCINETIA

Floral biology. *Freycinetia* inflorescences are borne on hapaxanthic axes, either terminating the major axis of the liana (*F. reineckei*, *F. marginata*) with renewal growth occurring from an axillary bud beneath the inflorescence, or terminating axillary shoots (*F. arborea*, *F. scandens*). In some species the shoots arise on defoliate branches (*F. funicularis*). The pattern of serial changes in leaf

form and size along the *Freycinetia* axis is similar to the pattern found in other monocotyledons (Kaplan, 1973), although the reduction in bract size toward the distal end of the axis is strikingly different from some Cyclanthaceae (Harling, 1958). The changes in leaf length, basal width, and the occurrence of marginal spines along a vegetative axis are illustrated in Figure 12. There is an increase in leaf length from the oldest leaf, the prophyll (leaf number 34) to the mature foliage leaves (leaf number 16) and thence a decrease in length to the youngest leaf (number 1), which encloses the meristem. If the axis terminates in an inflorescence, there is a distinct decrease in length and number of marginal spines toward the distal end (Fig. 12) with a smooth transition from foliage leaves to the fleshy bracts. Frequently foliage leaves immediately beneath the inflorescence have a patch of bright coloration at their base, which undoubtedly adds to the attractiveness of the inflorescence to potential pollinators. For an illustrated example of these transitions see Stone (1967).

In *Freycinetia angustifolia* and *F. jagorii* the inflorescence is clearly racemose. In all or most



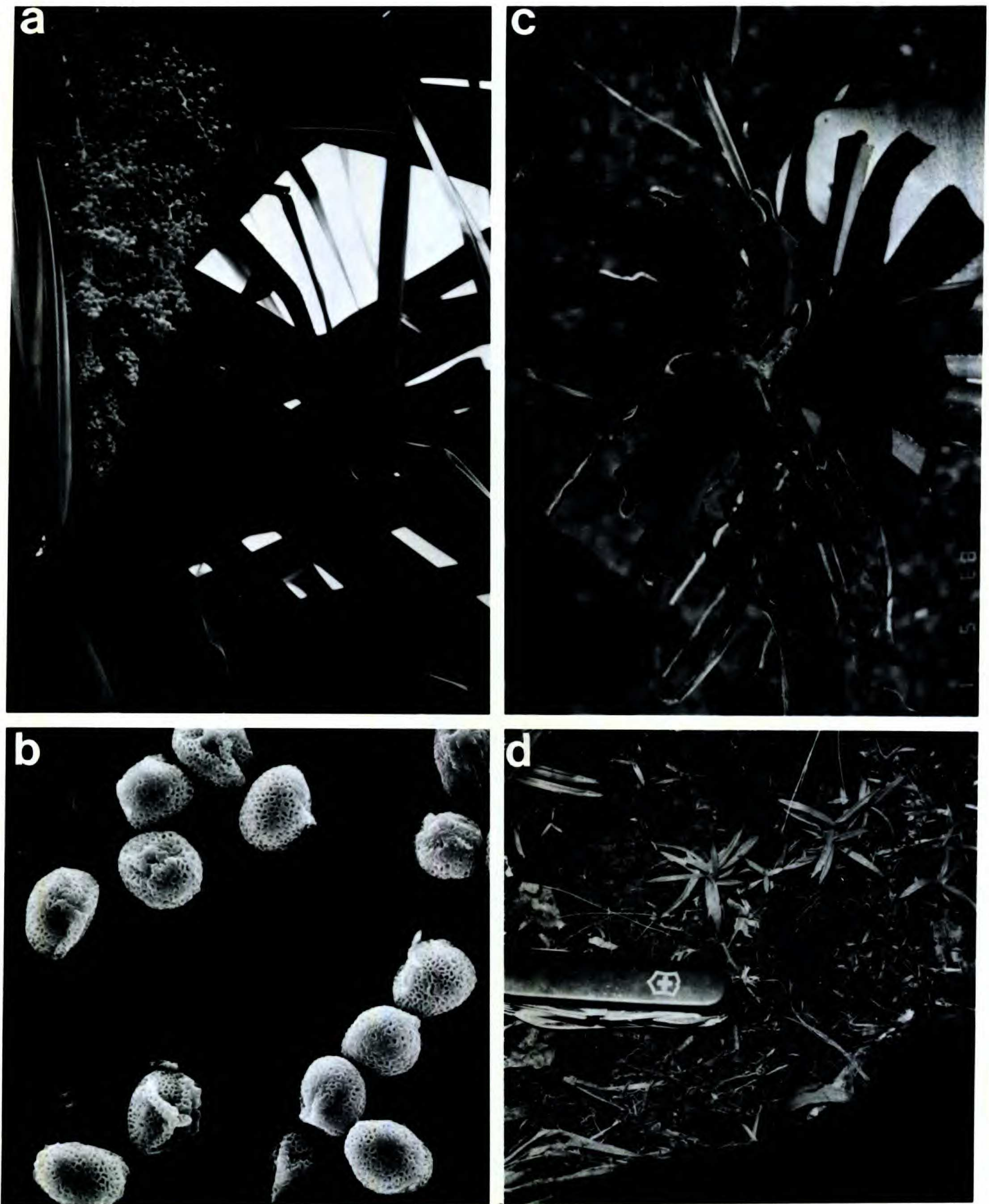


FIGURE 8. *Sararanga sinuosa* in the Solomon Islands.—a. Pendulous pistillate inflorescence in Tulagi.—b. Pollen.—c. Juvenile in Tulagi showing tristichous phyllotaxis.—d. Seedlings in Tulagi showing tristichous phyllotaxis.

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FIGURE 7. *Sararanga sinuosa* in the Solomon Islands.—a. Habit in Guadalcanal.—b. Root system in Tulagi; note absence of stilt roots.—c. Pistillate infructescence in Guadalcanal.—d. Cephalia in Guadalcanal.

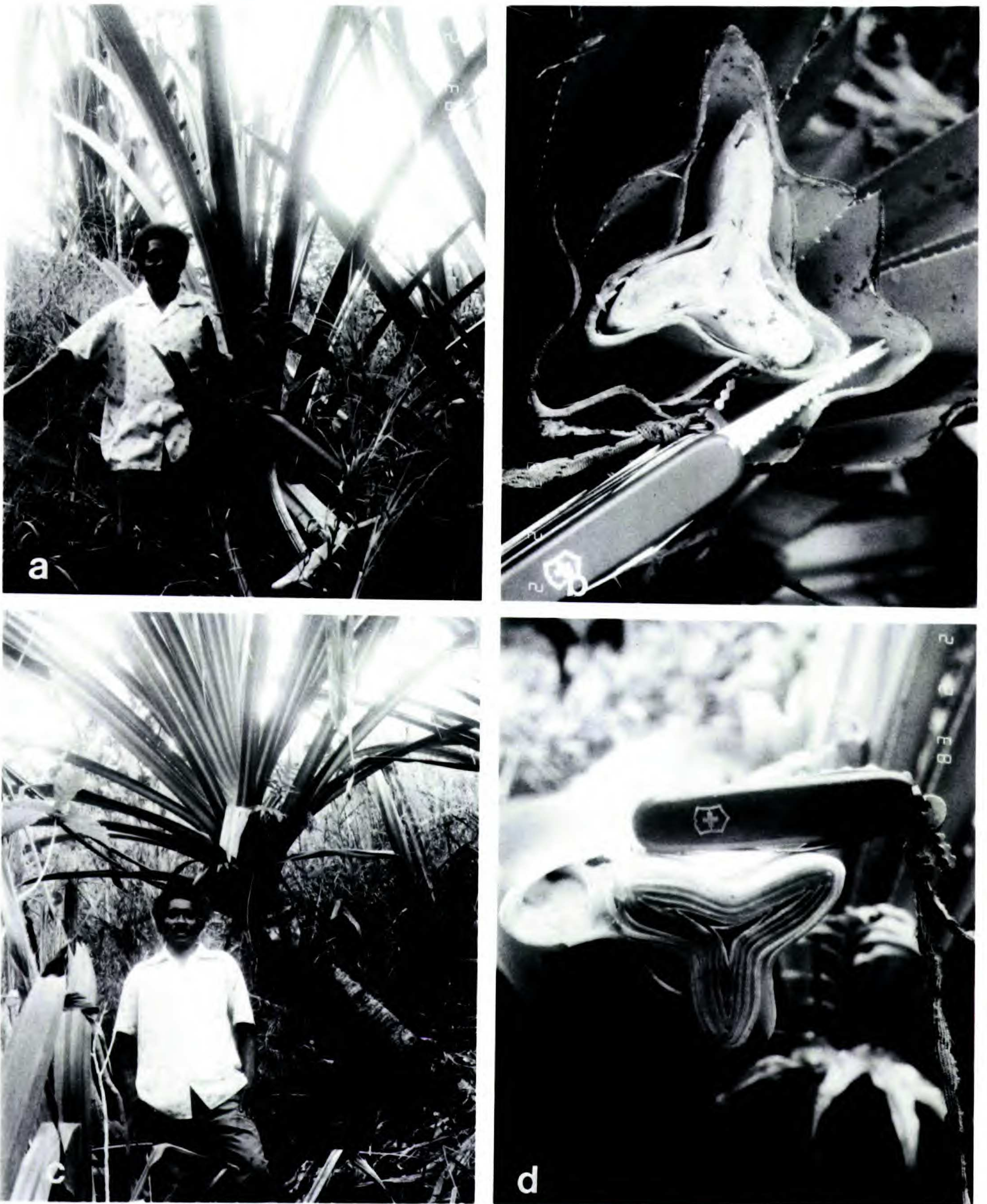


FIGURE 9. *Sararanga sinuosa* in Guadalcanal, Solomon Islands. —a. Juvenile. —b. Field dissection of “a” showing tristichous phyllotaxis. —c. Larger juvenile. —d. Field dissection of “c” showing tristichous phyllotaxis.

other species, the inflorescence is a false umbel of spikes with the subtending fleshy bracts telescoped by a reduction of internode length yielding the pseudoumbellate structure. Various colors are found in *Freycinetia* inflorescences. Some species have white bracts (*F. hombronii*, *F. scandens*), while

others have colored inflorescences ranging from pale salmon (*F. arborea*) to bright reddish orange (*F. reineckeii*, *F. marginata*) (Cox, 1984; Cox et al., 1984; Stone, 1982b). Some species have bright yellow bracts (*F. biloba*), while others have very dark purple bracts (*F. negrosensis*). Species with

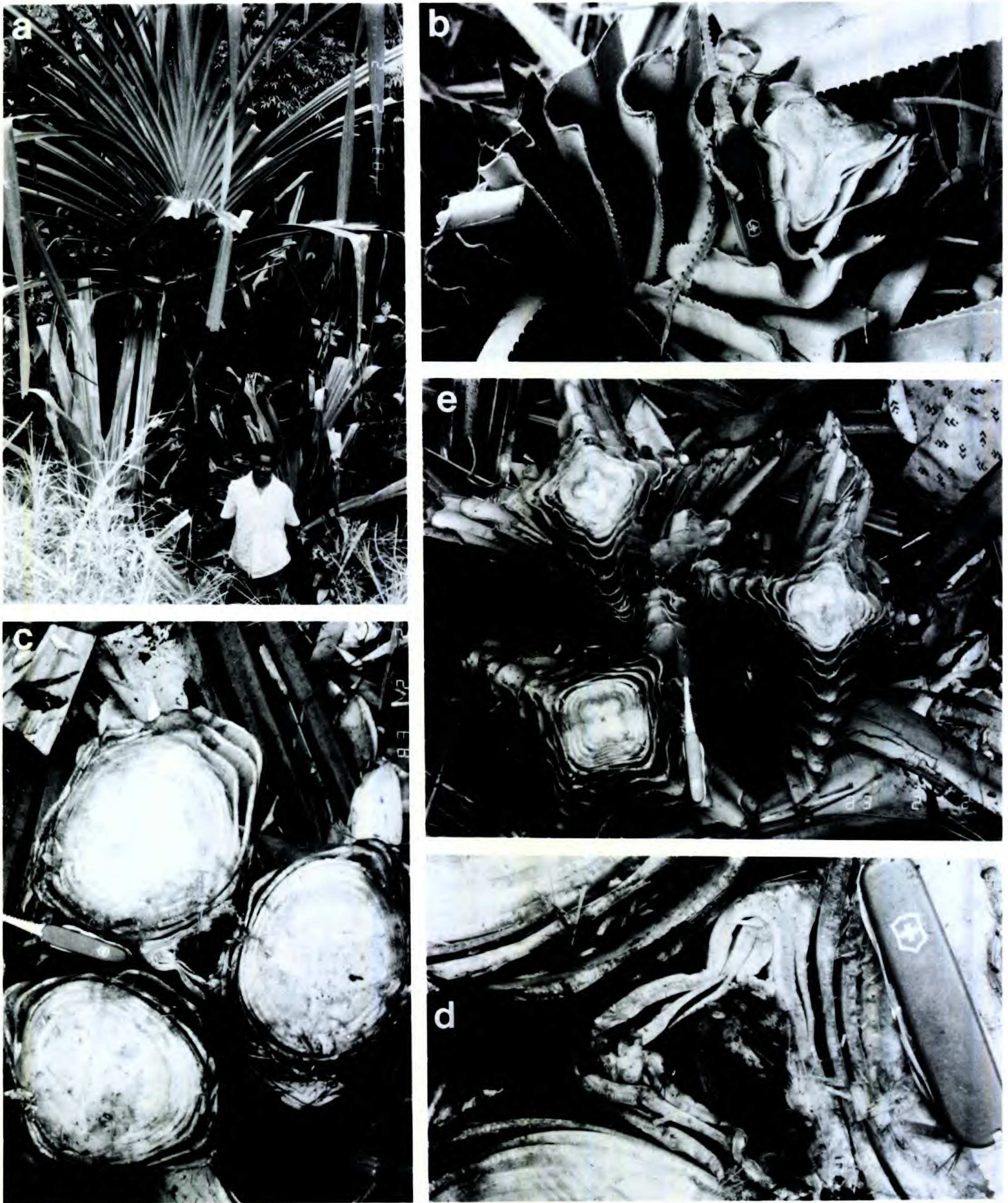


FIGURE 10. *Sararanga sinuosa* in Guadalcanal, Solomon Islands.—a. Large juvenile.—b. Field dissection of “a” showing tristichous phyllotaxis.—c. Field dissection of postreproductive individual, showing tristichous base of inflorescence and three axillary branches produced beneath inflorescence.—d. Close-up of tristichous inflorescence base.—e. Same three branches photographed prior to dissection stage shown in “c”; note superficial tetrastichy of branches.

white inflorescences produce a fetid, musky smell while those with colored inflorescences frequently lack a distinctive smell; however, this topic lacks substantive data as yet.

No liquid nectar is produced by *Freycinetia*

species. Instead, the bracts themselves function as hexose-rich “solid nectar,” containing up to 29% by dry weight total sugar (Cox, 1983) with particularly high concentrations of fructose (Cox, 1983, 1984; Cox et al., 1984). The bracts are also rich

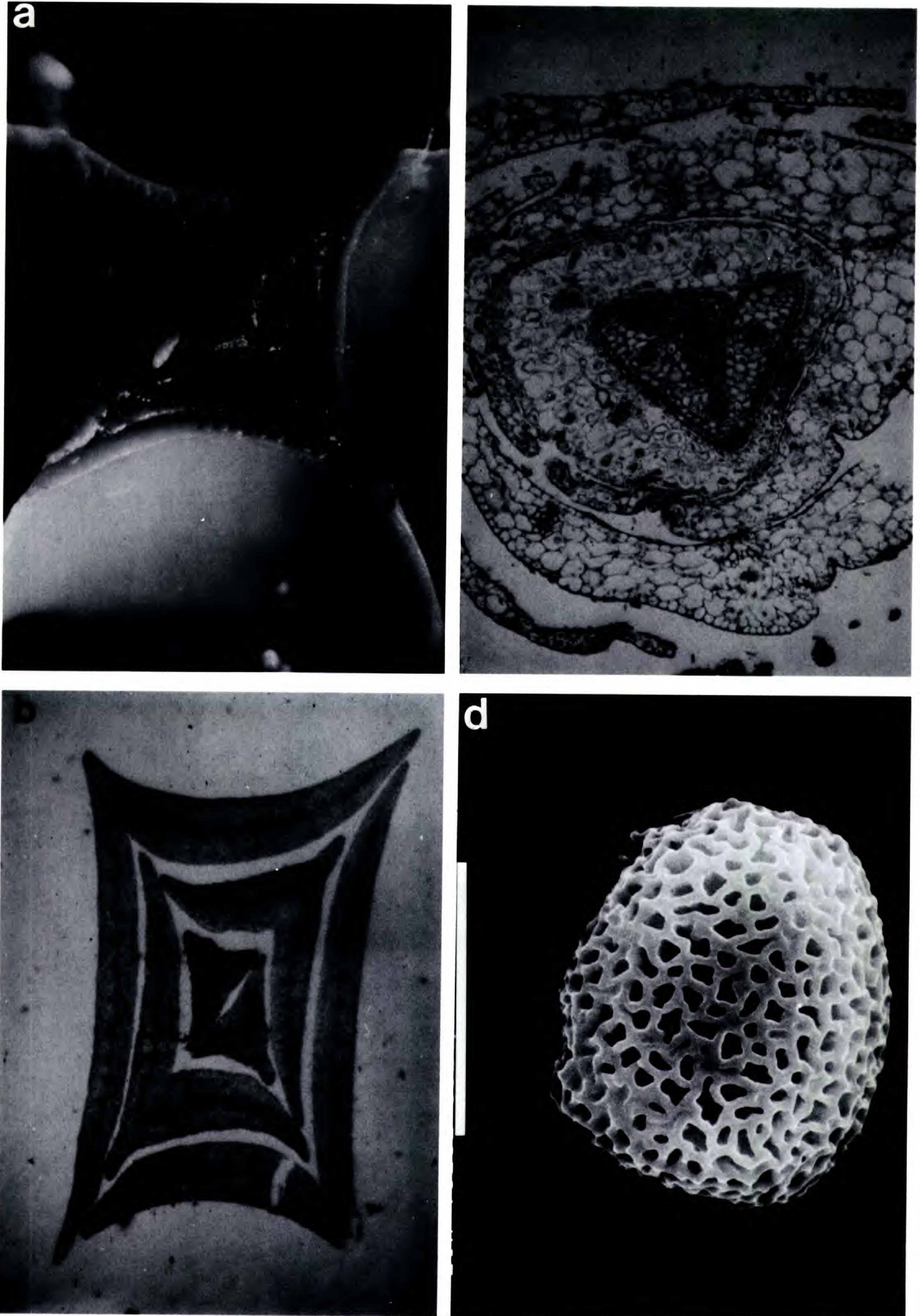


FIGURE 11. *Sararanga sinuosa*.—a. Superficially tetrastichous apex of branch produced subsequent to first flowering.—b. Cross section of "a" showing distichous nature of phyllotaxis.—c. Cross section of tristichous apex of prereproductive primary axis showing tristichous phyllotaxis.—d. Pollen with reticulate exine.

in free amino acids, with up to 9% by dry weight total amino acids (Cox, 1983), and up to 12 different amino acids present (Cox, 1984).

The number of spikes in an inflorescence usually varies between three and seven, while in *F. celebica*, the spike is usually solitary. Since each of these spikes is subtended by a fleshy bract, the shortening of internodes in this region of the axis permits the clustering of the spikes and bracts into a single anthecological unit that seems well adapted for vertebrate pollination (Fig. 6). The staminate spikes are often the same color as the distal bracts. The pistillate spikes, however, are usually green, though they may be white or pink in some species. The staminate spikes represent a high-quality reward for pollinators, as they may provide up to 26% dry weight crude protein and up to 24% dry weight lipid (Cox, 1984). Their high lipid content probably results in large part from the lipid-rich *pollenkitt* that covers the pollen.

At the terminus of the axis are several fleshy bracts (Bekonstigungskörper) that do not subtend spikes and that differ from outer bracts by being smaller and cylindrical, and by lacking marginal teeth on their tips.

The true flowers are extremely tiny and are congested on the spikes. The absence of perianth members at maturity makes delimitation of each flower very difficult, though their individuality can be discerned by studies of floral organogenesis.

Experimental. Developmental stages of *Freycinetia arborea* inflorescences were collected on the islands of Kauai and Hawaii and preserved in FAA. The spikes were bisected longitudinally. Half of each spike was stained in acid fuchsin, de-differentiated in 75% ethanol, and studied using the epi-illumination techniques of Sattler (1968). The other half was critical-point dried, coated with a silver-gold-palladium amalgam, and studied using the scanning electron microscope techniques of Uhl & Moore (1980).

With both techniques, floral units, each of which is subtended by a tiny bract (Fig. 13a), can be distinguished along the inflorescence. The outer whorl usually consists of six perianth primordia, inside of which is the whorl of androecial primordia (indicating six stamens). At a later stage of development (Fig. 13b), several gynoecial primordia develop inside the androecial whorl. In staminate spikes, however, the floral bracts, perianth, and gynoecium soon cease development (Fig. 13c) and only the androecial primordia continue developing, with the aborted gynoecial primordia forming a ring-shaped pistillode (Fig. 13d). Comparable developmental information for pistillate spikes is un-

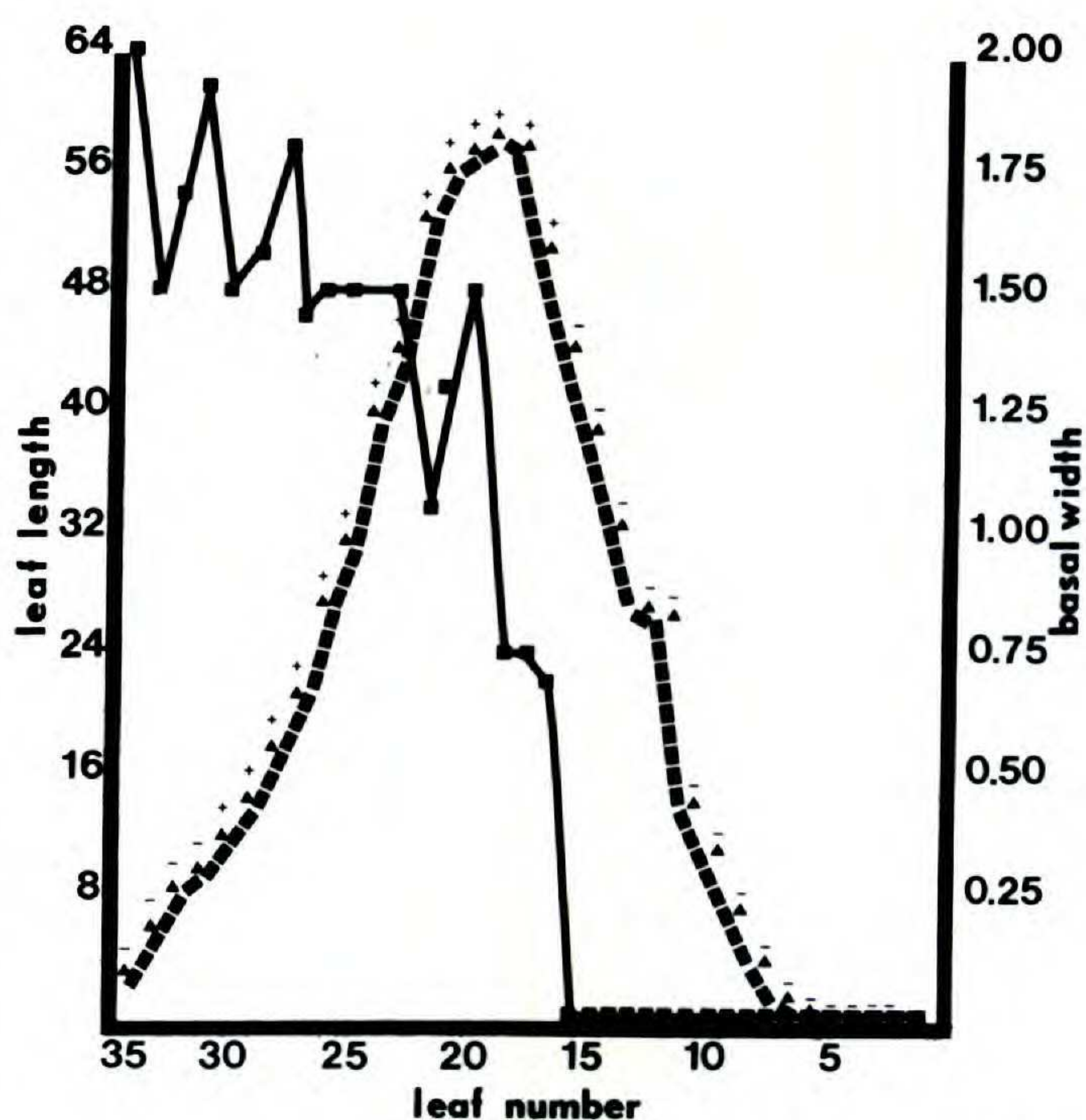
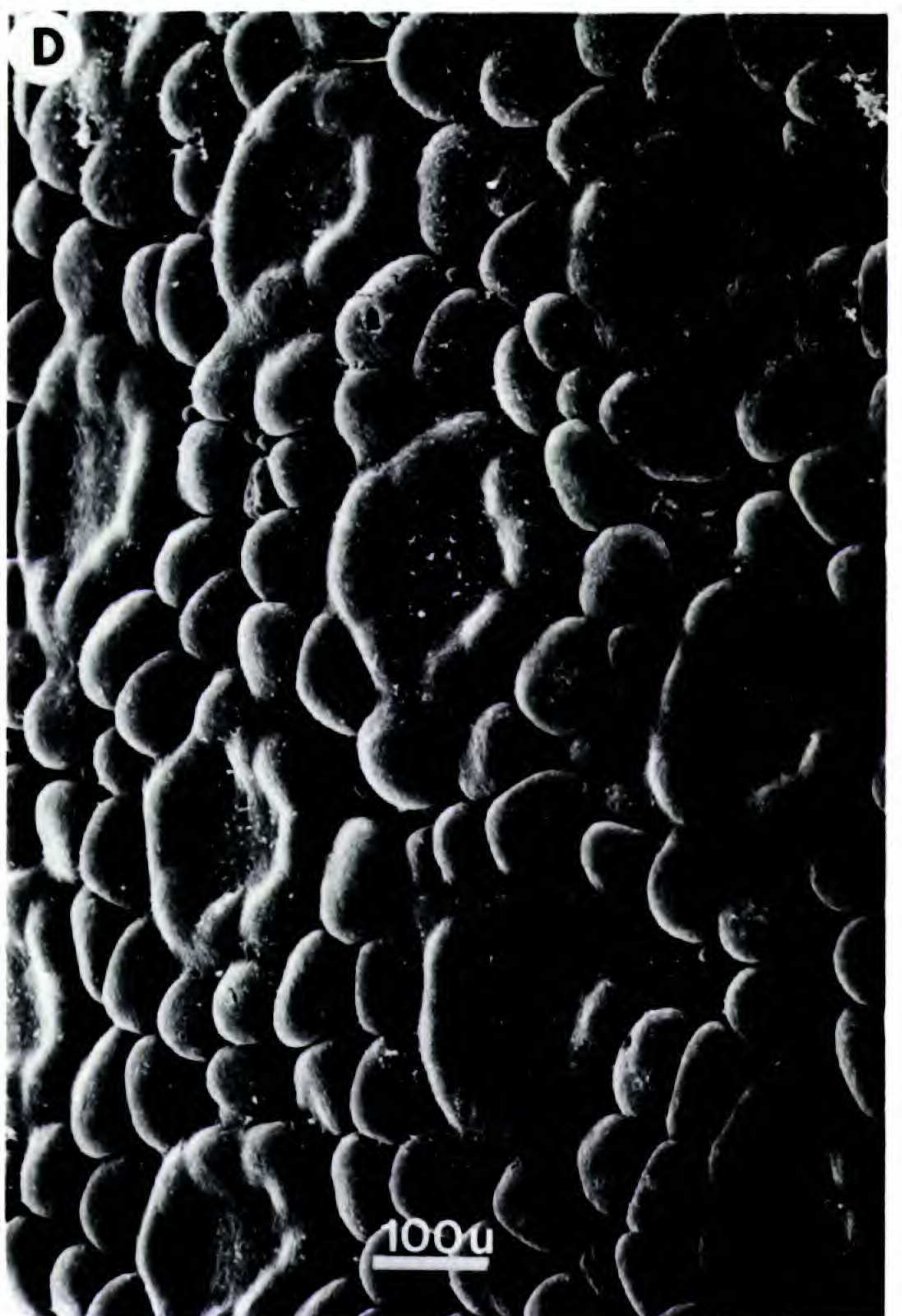
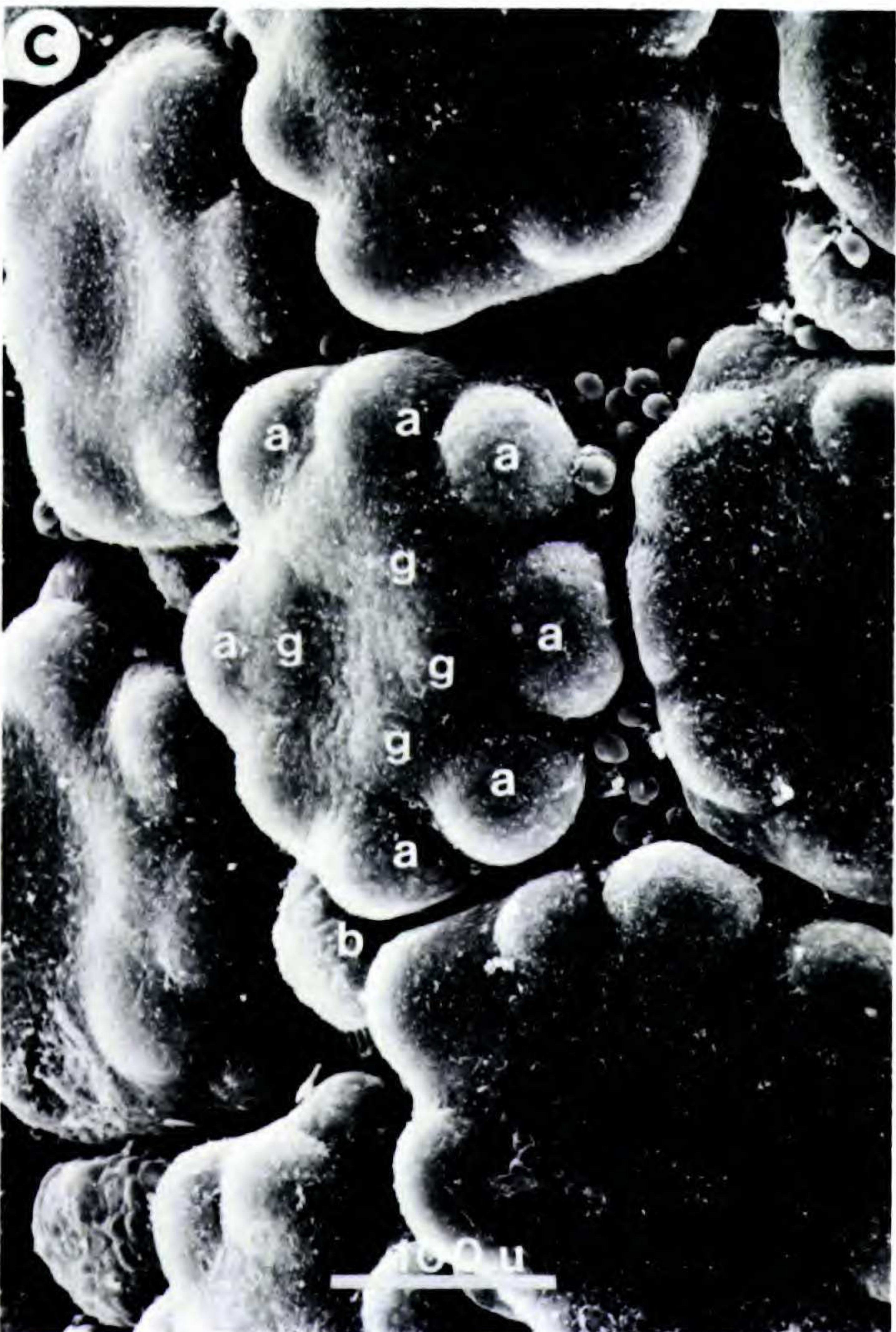
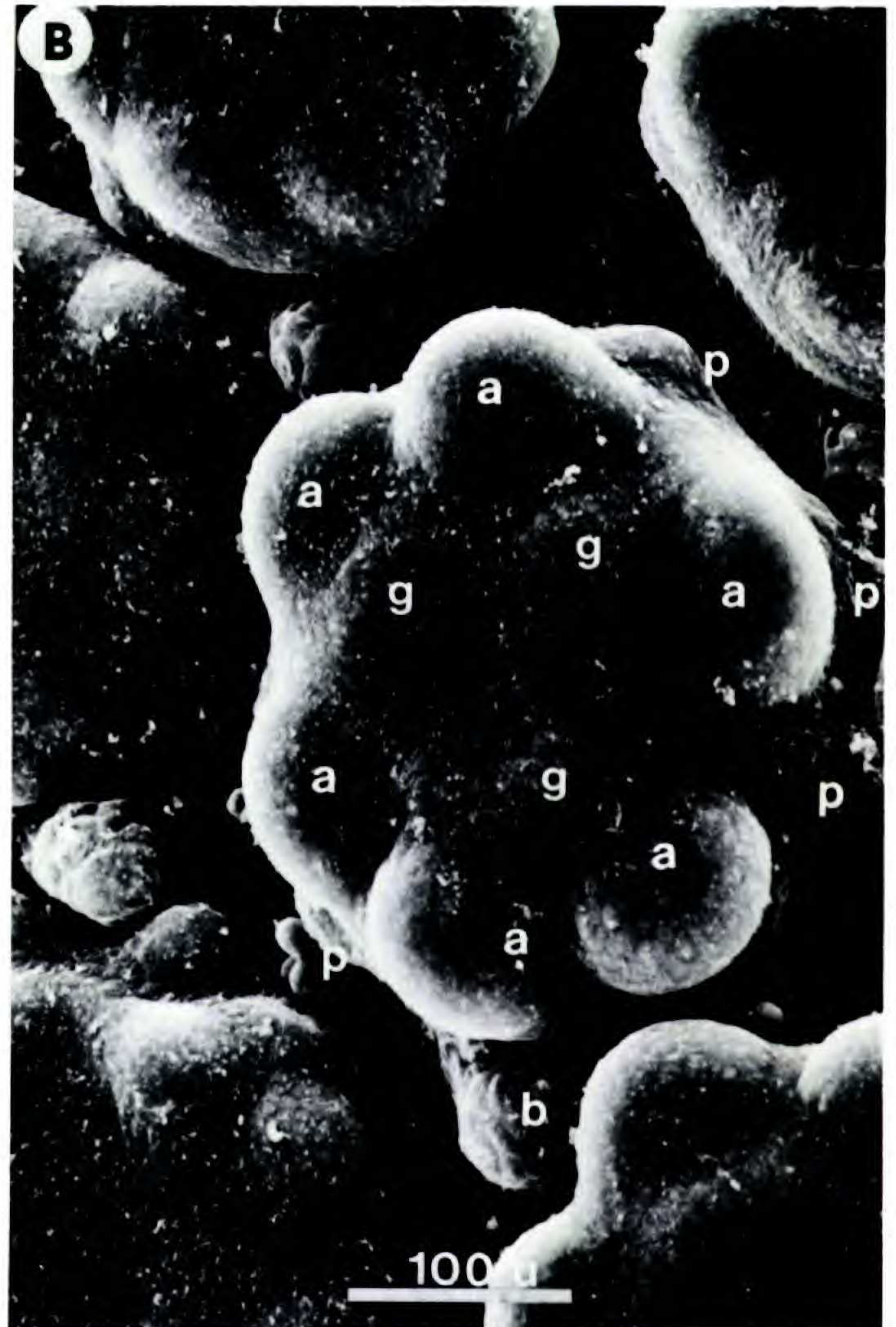
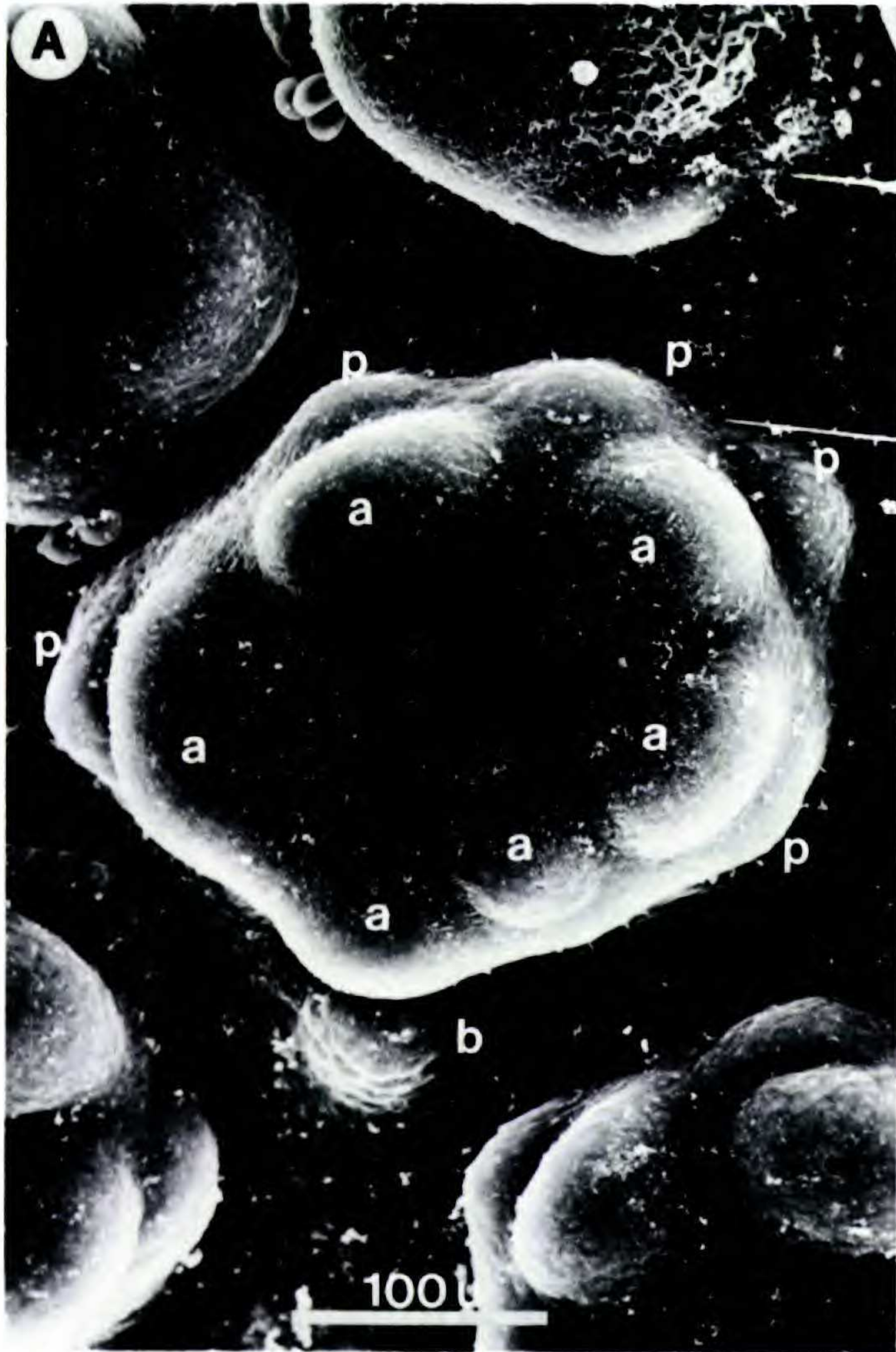


FIGURE 12. Leaves of transition along a vegetative axis of *Freycinetia reineckeii*. Dotted line indicates leaf length in centimeters; solid line indicates basal width in centimeters; + or - indicates presence vs. absence of marginal spines. Leaf 34 is the prophyll, with leaves 34-16 being mature; data on leaves 16-1 (the youngest leaf) were obtained by dissection of the apical bud.

available because the appropriate stages have yet to be collected; however, a similar sequence of events probably occurs since the mature gynoecia of many *Freycinetia* species are surrounded by numerous diminutive staminodia (Fig. 14).

Breeding systems. Although *Freycinetia* and all Pandanaceae have been believed to be strictly dioecious (Hutchinson, 1973; Dahlgren et al., 1985), recent fieldwork has indicated that a variety of breeding systems exists in *Freycinetia* (Cox, 1981; Cox et al., 1984; Poppendieck, 1987). To discuss this diversity and its evolutionary significance, it is useful to consider a *Freycinetia* individual as a metapopulation (White, 1979) of modules. More precisely, a *Freycinetia* (or any other) plant can be viewed as having modularity at different levels, thus being composed of a nested set of modular units (Cox, 1988). In all known species of *Freycinetia* a minimum of four levels of modular construction can be recognized. For example, entire genetic individuals (Fig. 15a) of *F. reineckeii* may be considered as modules at one level (let us call this level 1), and these modules could theoretically be either sexually monomorphic (all hermaphroditic) or dimorphic (pistillate and staminate). A second modular level (level 2) consists of hapaxanthic axes terminated by an inflorescence (Fig. 15b); again, these hapaxanthic axes can be sexually monomorphic or dimorphic. A third modular level



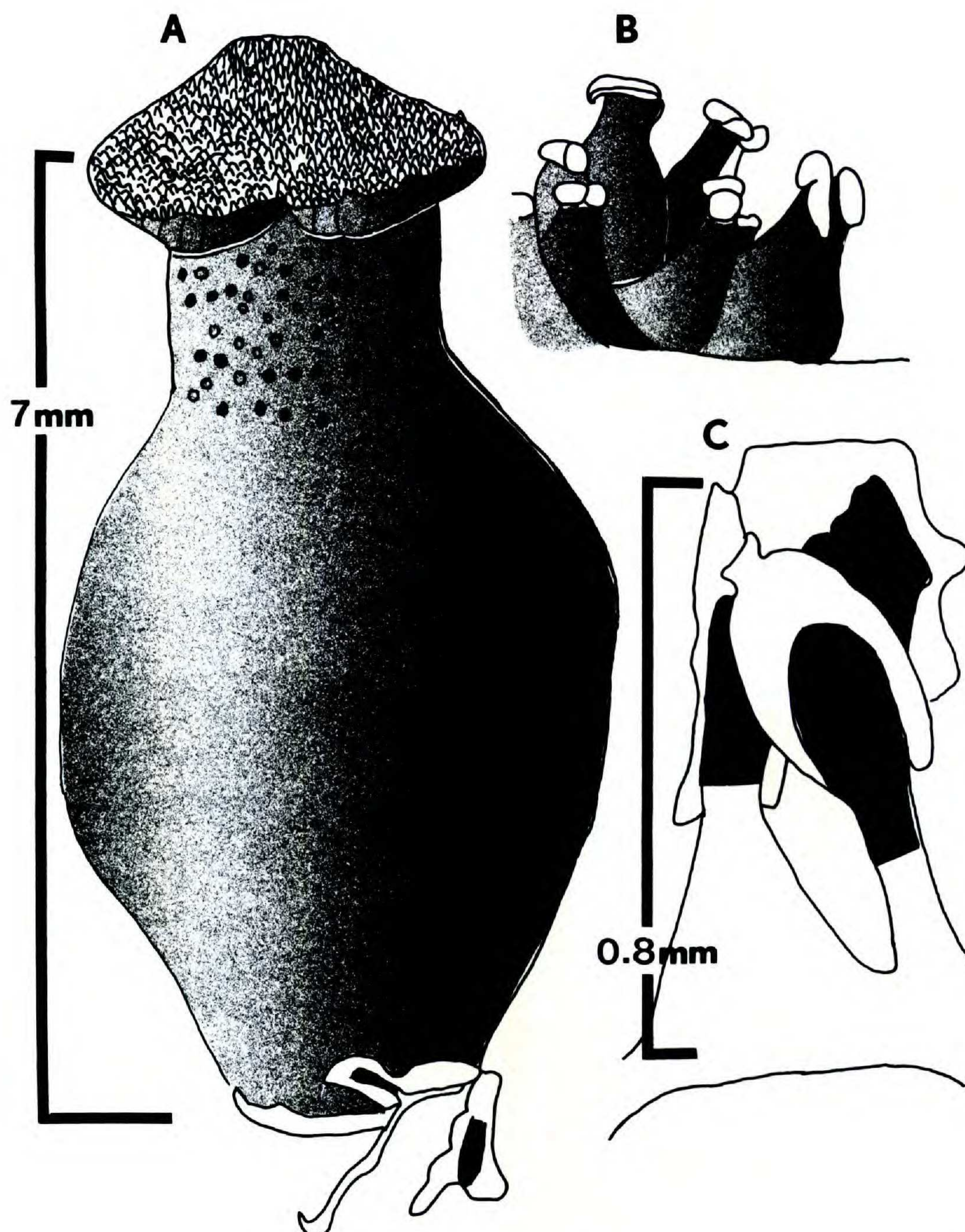


FIGURE 14. Gynoecial structures of *Freycinetia reineckei*.—A. Mature gynoecium with bilobed stigma, gland dots on ovary neck, and staminodia at ovary base.—B. Aspect of gynoecia on surface of spike.—C. Detail of staminodia.

(level 3), which may be either monomorphic or dimorphic, is the spike together with its subtending bract (Fig. 15c). Within each spike is found the fourth modular level (level 4), the floral unit subtended by a tiny bract (Fig. 15d), which could be sexually monomorphic or dimorphic.

For a *Freycinetia* species to be dioecious, i.e.,

sexually dimorphic at modular level 1, all lower modular levels also must be dimorphic. However, recent field research has revealed some individuals of *F. reineckei* in Samoa to be hermaphroditic at level 3 by producing hermaphroditic spikes (Cox, 1983), as are some individuals of *F. strobilacea* in Indonesia (Cammerloher, 1923; Stone, 1971).

←
FIGURE 13. Floral organogenesis in *Freycinetia arborea*.—A. Early developmental stage of flower with subtending bract (b), perianth primordia (p), and androecial primordia (a).—B. Later stage of development showing gynoecial primordia (g).—C. Subsequent developmental stage showing cessation of perianth development, and coalescence of gynoecial primordia into staminode.—D. Later stage showing several flowers along spike. Gynoecia, bracts, and perianth members have all ceased development with only androecial members continuing growth.

MODULAR LEVELS IN FREYCINETIA

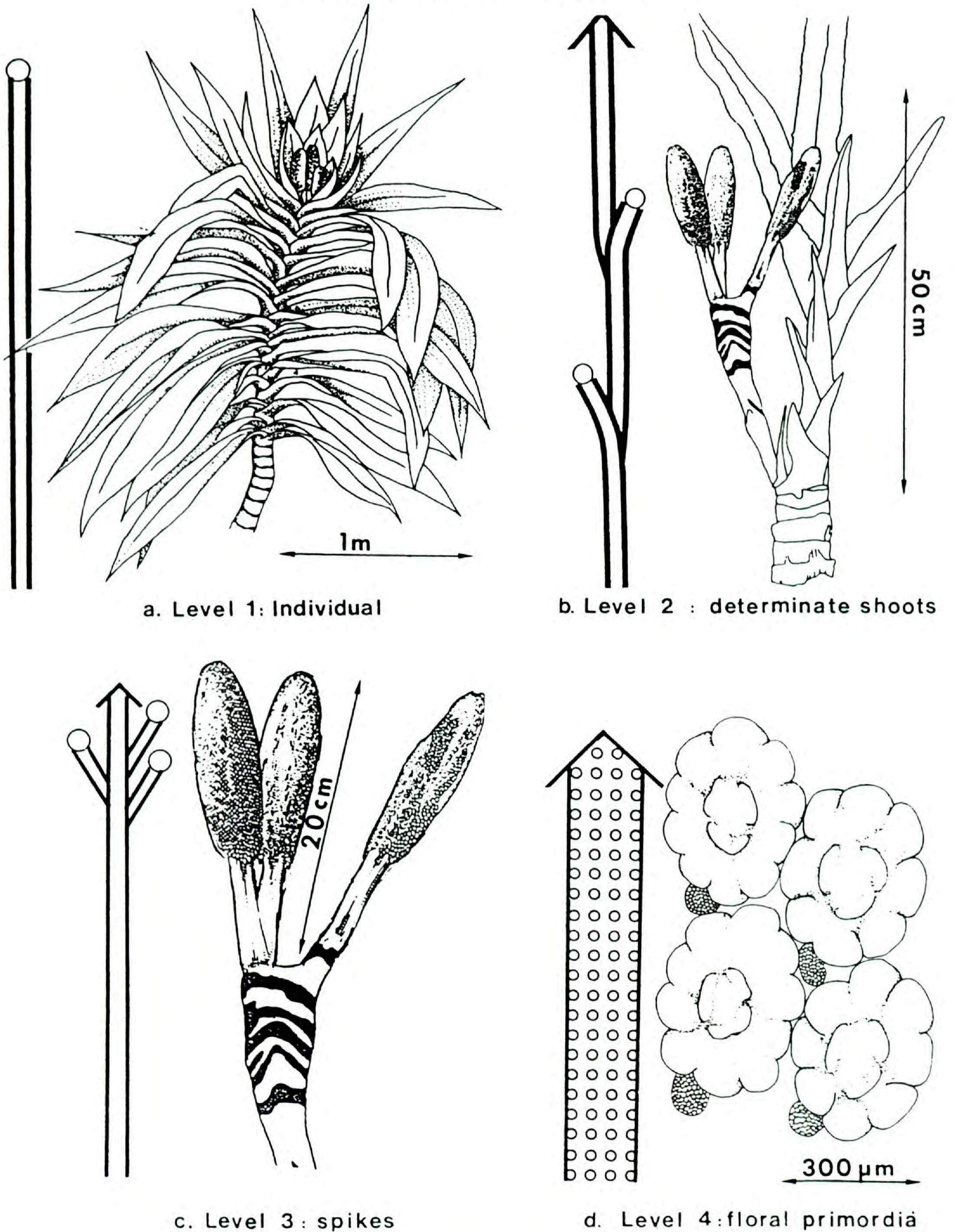


FIGURE 15. The different modular levels in *Freycinetia reineckeii* at which various dimorphic or monomorphic reproductive strategies could be expressed. The floral primordia in (d) occur early during organogenesis; crowding on the mature axis obscures individual floral units, particularly on staminate spikes.

Some individuals of *F. scandens* in Australia are hermaphroditic or monomorphic at level 1 by producing male and female shoots on the same plant (Cox et al., 1984); sexual monomorphism at this level is usually termed "monoecism." Similar cases of monoecism were described by Stone (Stone, 1972c; Cox, 1981) in individuals of *Freycinetia imbricata* in Sumatra and *Freycinetia negrosensis* in the Philippines, which also produce staminate and pistillate shoots on the same plant. Such divergences from a dioecious breeding system may be important in island colonization (Baker & Cox, 1984), particularly since monoecious individuals of *Freycinetia scandens* have been found to be self-compatible (Cox et al., 1984). Bagging and exclusion experiments for several species of *Freycinetia* indicate that apomixis is absent (Cox, 1983, 1984).

Pollination biology. *Freycinetia* inflorescences are adapted to pollination by several kinds of vertebrates such as flying foxes (Burck, 1892; van der Pijl, 1956; Cox, 1982, 1984); smaller bats (Knuth & Loew, 1904; Daniel, 1976); squirrels (Heidi, 1927); crows (Cox, 1983); pigeons (Cox, 1984); honeycreepers (Cox, 1983); and white eyes (Cox, 1983); but not rats (Cox, 1983). The openness and availability of the inflorescence to a wide taxonomic variety and size range of pollinators suggest a lack of tightly coupled plant-pollinator coevolution. Indeed, *Freycinetia* pollinators tend to be frugivores. Biochemical assays of *Freycinetia reineckeii* inflorescences and a variety of indigenous Samoan fruits eaten by its major pollinator, *Pteropus samoensis*, revealed striking similarities between hexose/disaccharide ratios and amino acid compositions (Cox, 1984). In contrast to pollination systems that are believed to have coevolved in other plants, no apparent evolutionary response of pollinators to *Freycinetia* has been found. There is, however, strong evidence that pollinator behavior has affected the evolution of breeding systems in *Freycinetia*.

The vertebrate pollinators of *Freycinetia* tend to be destructive. For example, the flying foxes that pollinate *Freycinetia reineckeii* in Samoa and Guam, *Pteropus samoensis* and *P. mariannensis*, respectively, eat the inner and outer staminate and pistillate bracts as well as the lipid-rich staminate spikes (Fig. 6c, d). Pistillate spikes, which are green and mucilaginous, are rarely disturbed and set abundant seed when pollinated. Although staminate spikes transmit their genes via pollen on the pollinators' faces, and pistillate spikes transmit their genes via ovules, hermaphroditic individuals lose a

large proportion of their investment in gynoecial structures due to pollinator damage, and they have a low fitness, represented by a concave fitness set (Cox, 1982). Quantitative comparison of the fitnesses of staminate, pistillate, and hermaphroditic individuals shows vertebrate pollination maintains the dioecious breeding system in *Freycinetia reineckeii* (Cox, 1982).

Dispersal. The infructescences of *Freycinetia* are usually brightly colored, frequently red, and are rich in sugars. These attributes make them attractive to various birds and perhaps some flying foxes. *Freycinetia reineckeii* in Samoa is dispersed by *Aplonis artifuscus* (Sturnidae). *Fauna Hawaiiensis* (Perkins, 1902) is filled with references to birds of various genera eating *F. arborea* fruits. Guppy (1906) believed birds to be the primary dispersers of *Freycinetia* species and reported finding bird pellets below the inflorescences filled with *Freycinetia* seeds. Experiments on seed germination (Cox, unpublished) suggest adaptation to endozoochoric dispersal, since *F. reineckeii* seeds require a mild acid treatment for successful germination. Dispersal by flying foxes is undoubtedly important as well. The type specimen (at BISH) of *Freycinetia degeneri* (Degener 15128) has written on the label, "fresh roots pounded as roofs to build their grass houses. They do not eat fruit. Flying foxes eat it." Smith (1979) also believed flying foxes to be important dispersal agents in Fiji. Terrestrial mammals also probably aid dispersal; Perkins (1902) reported that rats eat *F. arborea* in Hawaii, and they are implicated as seed dispersers in New Zealand. A specimen of *F. banksii* (Meebold 18245) has written on the label, "eaten by rats," which Daniel (1973) confirmed. The attractiveness and availability of *Freycinetia* infructescences to a wide variety of vertebrates has perhaps been best stated by Stone (1970, pp. 85–86): "Probably the fruits—technically berries—are dispersed by birds, bats, and possibly other mammals. Being juicy, they are edible."

PANDANUS

Floral biology. Stone (1968b) grouped pistillate inflorescences of *Pandanus* according to whether the cephalia are solitary or multiple, and whether the fruits are free or connate into syncarps. In species with single cephalia (e.g., *P. tectorius* sensu latissimo, *P. leram*, Stone, 1983), numerous chartaceous bracts, usually pale yellow or white, are produced beneath the inflorescence and are inserted tristichously. In species with multiple cephalia (e.g., *P. nepalensis*, *P. spinistigmaticus*),



FIGURE 16. *Pandanus tectorius*. —a. Habit in Maui. —b. Staminate inflorescence in Moorea.

the cephalia are borne on racemes, and beneath each cephalium is a single bract. *Pandanus* species in general do not show the extreme telescoping of the main inflorescence internode that occurs in *Freycinetia*, although the cephalia themselves reveal much telescoping of secondary and tertiary axes. Staminate inflorescences of *Pandanus* usually consist of panicles of staminate spikes, each spike subtended by a large, often pale-colored bract. Floral units homologous to those found in *Freycinetia arborea* have yet to be discovered in *Pandanus*, but those of *P. androcephalanthos* and other species of subg. *Martelidendron* in Madagascar perhaps have a similar construction. Stamens are usually fasciate in phalanges, pistillodia infrequently occur (e.g., *P. douglasii*, Stone, 1968b), but tepals have yet to be identified. Similarly, staminodia infrequently occur in pistillate *Pandanus* individuals (e.g., *P. cominsii*, Stone, 1968b), but again tepals have yet to be identified. Detailed studies of floral organogenesis in *Pandanus* are needed.

Pandanus inflorescences, particularly staminate inflorescences (Fig. 16), sometimes have a subtle, pleasant fragrance. Indeed, staminate inflorescences of cultivated *P. odoratissimus* are used in

India as a base for perfumes, the “oil of Keura” (Purseglove, 1972). Neither sex, however, produces nectar, and fleshy bracts similar to those found in *Freycinetia* are unknown.

Breeding systems. A true departure from strict dioecism in *Pandanus* has yet to be found. Given the widespread occurrence of staminodia and pistillodia (Stone, 1968b) in the genus, however, it seems likely that further field studies will reveal aberrations. For example, Stone (1972b) found two pistillate individuals of *Pandanus cominsii* var. *Augustus* on Buka Island that had drupes surrounded by staminodia, some of which had anthers; *P. microcarpus* produces staminodia with anthers adnate to the exocarp (Vaughn & Wiehe, 1953). Departures from strict dioecism, if they occur, either are extremely rare or are limited to certain species; I have yet to find, despite extensive searches throughout Polynesia, a single individual of *Pandanus tectorius* that produces both staminate and pistillate inflorescences.

Bagging experiments in Kauai and Maui, Hawaii, and Moorea (French Polynesia) indicate that

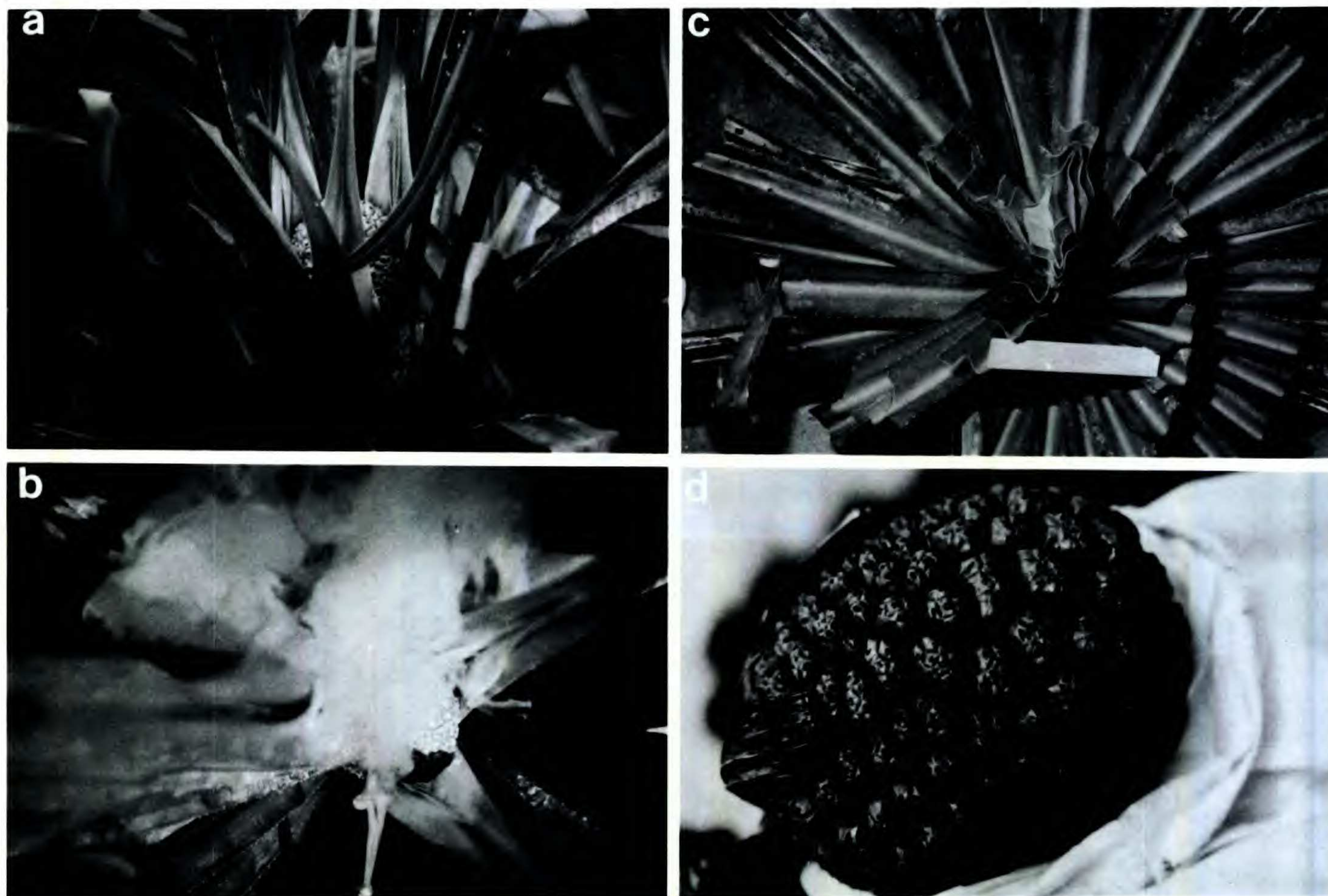


FIGURE 17. *Pandanus tectorius*.—a. Pistillate inflorescence.—b. Flow visualization in field showing deceleration near cephalium.—c. Tristichous phyllotaxis with secondary spiral.—d. Bagged cephalium indicating apomictic nature of breeding system.

Pandanus tectorius is facultatively apomictic (Cox, 1985). All bagged inflorescences produced fruit (Fig. 17). Possibility of contamination of the bags was checked with scanning electron microscopy of stigmatic surfaces; no pollen grains were found. Parthenocarpic fruit development was rejected since bagged cephalia produced viable embryos and endosperm. To determine whether apomixis was obligate or facultative, the genetic diversity of samples of endosperm from bagged and unbagged cephalia was studied with starch gel electrophoresis (Cox, 1985). Five different loci were examined. Endosperm samples from different syncarps from the same unbagged cephalium had significant isozyme diversity, while endosperm samples from syncarps from the same bagged cephalium were monomorphic at all loci. Thus the system is facultatively apomictic, with asexual reproduction occurring in the absence of pollination. Campbell (1911) noted migration of somatic nuclei into the embryo sac, which was confirmed by Cheah & Stone (1975), who found supernumerary nucellar nuclei in the embryo sac of *Pandanus parvus*. Facultative apomixis may occur throughout the genus; as early as 1867 Kurz found isolated *Pandanus dubius* females to produce fruit, while Fagerlind (1940) reported apparent parthenocarpy in *Pandanus co-*

lumniformis. I have found in the Royal Botanic Gardens, Sydney, a sole pistillate individual of *Pandanus forceps* that sets abundant fruit, and in the Royal Botanical Garden, Melbourne, a single pistillate individual of *Pandanus forsteri* that also produces copious fruit; whether this indicates apomixis or parthenocarpy remains to be determined.

Pollination biology. The pollination biology of nearly all species of *Pandanus* remains unstudied. I have made an extensive study, however, of the pollination ecology of *Pandanus tectorius* sensu latissimo in Hawaii and French Polynesia (Cox, 1985). Although insects (e.g., bees) are frequent visitors to staminate inflorescences where they gather pollen, they seldom visit pistillate inflorescences. Neither type of inflorescence produces nectar or any pollinator reward other than pollen. Peroxidase assays indicate an early onset of stigmatic receptivity that extends until well after fruit formation. The copious pollen produced by the pendulous, paniculate staminate inflorescences (Fig. 16b) is devoid of a *pollenkitt* and blows easily in the wind. However, a *pollenkitt* occurs in other species; according to Stone it is formed in *Pandanus beccarii* and similar species of sect. *Maysops*. To test for wind pollination, flow patterns

around pistillate inflorescences were examined with a laboratory wind tunnel using the techniques of Niklas (1982), and in the field using a portable smoke-injection apparatus (Cox, 1985). Regardless of inflorescence orientation, flows in the range of 1 m/sec. resulted in back eddies that caused significant deceleration in the region of the stigmatic surfaces (Fig. 17b). Spiral patterns in the xy and xz planes indicated that pistillate *Pandanus tectorius* inflorescences function as highly efficient pollen receivers, being hydrodynamically analogous to some filter-feeding marine invertebrates. This anemophilous nature of *P. tectorius*, together with its system of facultative apomixis, was confirmed through bagging studies.

Dispersal. The primary unit of dispersal on most *Pandanus* species is the syncarp, frequently termed a phalange.³ The phalanges are brightly colored, and the basal part is sweet. In coastal species, such as *P. tectorius*, the phalanges are buoyant and can frequently be found in beach-drift throughout the Pacific (Gunn & Dennis, 1976). Guppy (1906) and Ridley (1930) considered *P. tectorius* to be dispersed primarily by ocean currents, although Lee (1985) reported localized dispersal by crabs. Bird dispersal of *P. tectorius* also occurs in Samoa, and flying fox dispersal has been observed in Micronesia (Stone, pers. comm.).

Stone (1982a, pers. comm.) reported turtle dispersal of *P. helicopus*, a freshwater species, in the Malay Peninsula, and endozoochoric dispersal of inland species is highly likely (Stone, 1982a). Dispersal by humans of economically useful species has occurred as well.

In Hawaii a census of four 0.25-m² plots of *P. tectorius* phalanges lying on the ground revealed that of those phalanges that produce seedlings, 69% produce two–six seedlings (Cox, 1985). Using data from this survey, a probability analysis revealed that the likelihood of any established phalange producing at least one male and one female seedling exceeds 55% (Cox, 1985). Further work by Lee (1989) in Moorea has confirmed that the dispersal of a single phalange may establish a sexually reproductive population.

³ Terminology follows Stone. The levels employed are (1) carpel, (2) phalange, and (3) cephalium. Older works use syncarp, but this can refer to either level 2 or 3. Each carpel ripens to form a drupe; in species with free or solitary drupes, the cephalium consists of drupes. However, in species such as *P. tectorius*, each phalange is formed of several connate drupes; hence the term “poly-drupe” is sometimes used.

SARARANGA

Floral biology. The massive (up to 1.7 m long) pendulous inflorescences of *Sararanga* are always terminal (Figs. 14c, 15a), with renewal growth occurring through the development of axillary buds beneath the inflorescence. In contrast to *Freycinetia* and *Pandanus*, the pistillate inflorescence is strongly paniculate while the staminate inflorescence consists of panicles of staminate heads, similar to that found in *Pandanus* species. Both types of inflorescences are subtended by small, hard bracts. The nature of the terminal floral unit in *Sararanga* remains unclear. The green, terminal floral units (Fig. 7d) are composed of numerous fused carpels, each producing a single anatropous ovule beneath a single pointlike stigma. The sinuous arrangements of the fused carpels and their stigmas “strongly resemble the [pattern of] stitching on an American baseball” (Stone, 1961). A small, whitish cuplike structure is produced at the base of the fused carpels. This structure, when analyzed by paper chromatography, proves to be rich in hexose sugars. Although the terminal floral units were termed “receptacula florifera” by Hemsley (1893), Stapf (1896) called them flowers, a practice followed by Stone (1961), who considered the terminal floral units “pedicellate flowers” with the white cupule termed a “perianth.” North & Willis (1971) described the fertilized terminal floral units as “fleshy fruits, consisting of numerous carpels.”

However, precise homology between the terminal floral units of *Sararanga* and floral structures of other Pandanaceae, as well as other monocotyledons, remains obscure. Studies of floral organogenesis previously described revealed little similarity between the terminal floral units of *Sararanga* and the flowers of *Freycinetia*. Particularly unclear is the nature of the white cupule that subtends the terminal floral unit. This cupule scarcely resembles the perianth of any other monocotyledonous flower; it is much more bractlike in appearance. Ultimate resolution of these difficulties requires, in my opinion, study of the ontogenetic development of these structures; as yet, however, I have been unable to obtain the appropriate developmental stages (Fig. 18). Based on current information, the possibility that the terminal floral unit of *Sararanga* may be homologous to a *Pandanus* phalange, or even homologous to an entire *Pandanus* cephalium or *Freycinetia* spike, with the cupule representing the subtending bract, cannot be excluded. The fleshy cupule appears to serve the same function, as pollinator rewards, as the fleshy bracts of *Freycinetia*. Analysis of the cupule

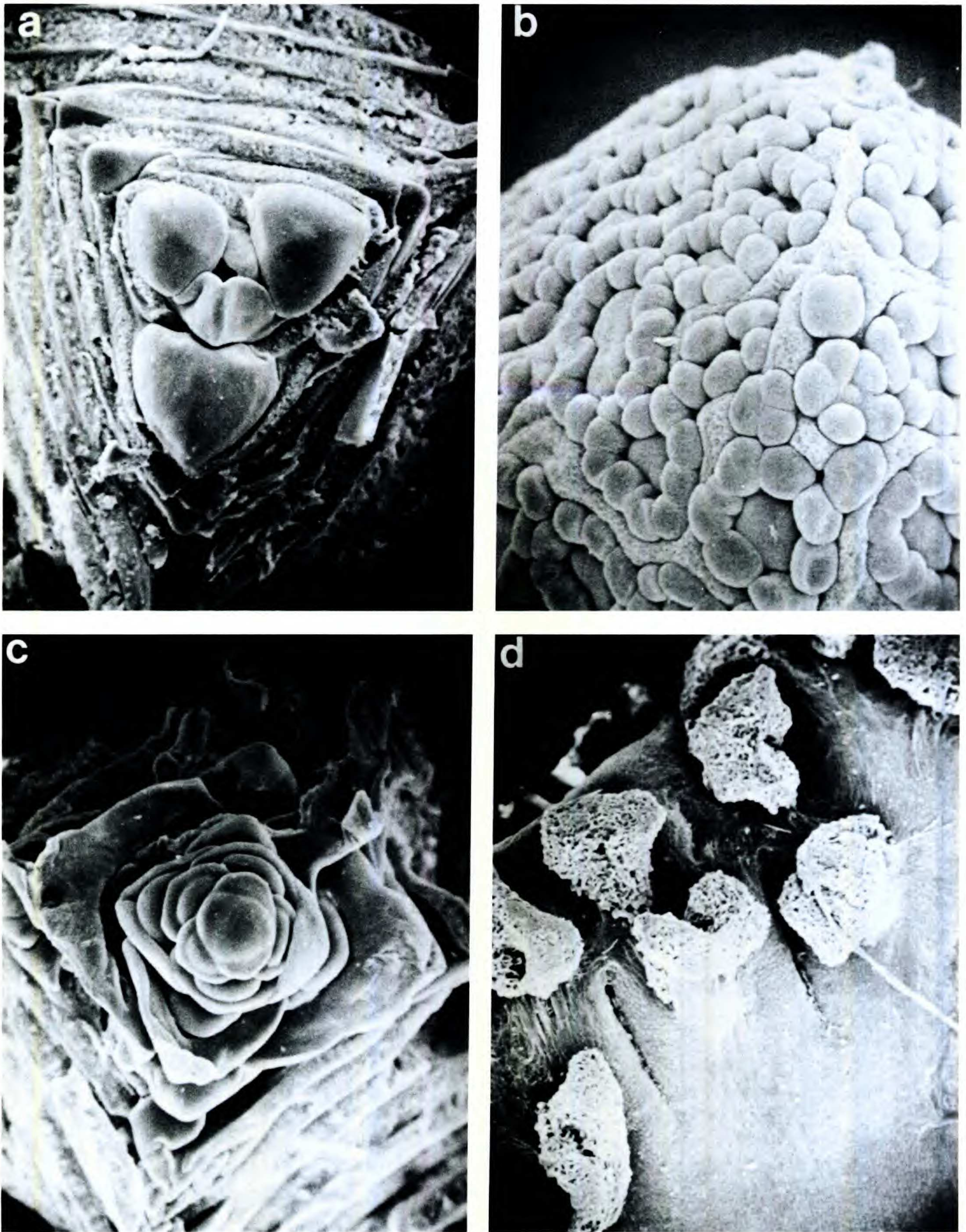


FIGURE 18. Floral organogenesis in *Freycinetia* and *Sararanga*.—a. Dissection of reproductive apex of *F. reineckei* showing young spikes and subtending bracts.—b. Early developmental stage of a staminate *F. reineckei* spike.—c. Dissection of *Sararanga sinuosa* reproductive staminate apex from a secondary axis showing early stages of inflorescence development; note decussate nature of phyllotaxis.—d. Stigmatic surfaces of *Sararanga sinuosa* cephalium.

reveals it to be similar to *Freycinetia* bracts by being very rich in hexose sugars. Since *Sararanga* produces no nectar or other pollinator reward, these white, fleshy cupules serve as the sole pollinator reward. They are, however, extremely small in comparison with the hexose-rich bracts of *Freycinetia* or the bracts of *Pandanus* inflorescences.

Breeding systems. I have surveyed populations of *Sararanga sinuosa* in the Konnga Region of Guadalcanal Island, Tulagi Island, and along the Siota Passage on Big and Little Ngela islands and have yet to discover any departures from strict dioecism. Staminodia and pistillodia are unknown in the genus.

Sararanga sinuosa does not appear to be apomictic, as some isolated trees have very poor or no fruit set, and within any particular inflorescence, numerous terminal floral units fail to develop. An isolated pistillate tree in the Honiara Botanical Gardens, Guadalcanal, sets some fruit, although the set is poor compared with wild trees. Because of deforestation, this individual is at least 6 km from any other possible conspecific and 15 km from any other known conspecific. Even this does not, however, provide evidence for apomixis or parthenocarpy, since, as will be discussed below, *Sararanga sinuosa* appears to be entomophilous. As Kerner von Marilaun (1895, p. 208) reported, a *Draunculus creticus* (Araceae) planted in the Vienna Botanic Gardens attracted at anthesis a swarm of dung beetles when previous to its opening none could be found anywhere in the Gardens or immediate vicinity. The possibility that the massive inflorescences of *Sararanga*, which rival those of the monocarpic palms in size and productivity, could attract pollinators from several kilometers away cannot be discounted.

Pollination biology. The pollen grains of *Sararanga sinuosa* average 13 μm in diameter, have reticulate exines (Figs. 15b, 18d), and lack a *pollenkitt*. The anthers are borne in groups, each of which is subtended by a small fleshy bractlike cupule nearly identical to that produced beneath the pistillate terminal floral units. As mentioned above, this cupule or bract is rich in hexose sugars. The entire staminate inflorescence has a slightly peppery smell; no similar odor can be detected from the pistillate inflorescences. The sessile stigmas of the pistillate floral units, borne in sinuous rows (Fig. 7d, 18d), show peroxidase activity while the unit is small and green. In staminate and pistillate inflorescences no nectar is produced; the sole pollinator rewards are pollen and the whitish, hexose-rich cupules or bracts that subtend the floral units.

Since the inflorescences are pendulous from the tops of these tall (20 m) trees, determination of floral visitors is difficult. I have witnessed small beetle-like flying insects visiting the pistillate inflorescences but have not captured any for identification and analysis. A night I spent in the crown of an *S. sinuosa* tree in Tulagi Island similarly failed to yield any evidence of nocturnal visitors. Wind tunnel analysis of flow patterns around pistillate inflorescences indicated no significant eddies or flow patterns produced by the inflorescence or by the terminal floral units that cause flow deceleration near the stigmatic surfaces. I therefore believe *Sararanga sinuosa* to be pollinated solely by flying insects, although further fieldwork in the Solomons is needed to gain more details of the pollination ecology of *Sararanga*.

Dispersal. Guppy (1906, p. 156) believed *Sararanga sinuosa* to be bird-dispersed. Although I have yet to witness dispersal, the bright red (A. D. E. Elmer called them "candy red") terminal floral units, which are rich in disaccharides, have a delicious taste reminiscent of cherries or strawberries. Given the position high in the trees, they are almost certainly dispersed by birds and bats, although confirmation of this awaits further fieldwork.

BREEDING SYSTEMS, EVOLUTION, AND SYSTEMATICS

In principle, the phylogenetic tree derived from systematic information can be used to interpret evolutionary trends in breeding system and pollination syndromes in the three genera of Pandanaceae. For example, because pollination syndromes appear to be relatively constant within each genus (with the exception of possible chiropterophily in some species of *Pandanus* sect. *Maysops*), and since each pollination syndrome obviously has an evolutionary history, the genera can be replaced with their respective pollination syndromes as shown in Figure 19. This modified cladogram indicates that within Pandanaceae, wind and insect pollination have evolutionary histories more closely related to each other than either does to vertebrate pollination. Only a few details concerning possible trends in pollination biology can be derived from the consensus tree, however, since information from pollination biology was not used to derive the tree. Unfortunately, the pollination biologies of three genera I have used as outgroups, *Balaka*, *Rhaphidophora*, and *Asplundia*, remain unknown. However, to illustrate the possibility for interpreting the evolution of breeding systems and pollination syndromes, should the sister group of the

Pandanaceae be convincingly demonstrated, I substitute for *Asplundia* in Figure 20 the genus *Cyclanthus* (Cyclanthaceae) whose pollination biology has been well studied (Beach, 1982).

In Costa Rica, *Cyclanthus bipartitus* is pollinated primarily by beetles (Beach, 1982). The first night after pistillate anthesis, scarab beetles of the genus *Cyclocephala* forage on the lipid-rich fleshy adaxial surfaces of the inner bracts. Later, after staminate anthesis, the beetles feed on the pollen.

If we put these details on the cladogram (Fig. 19), we find *Cyclanthus* and Pandanaceae sharing two features of pollination biology as a symplesiomorphy: fleshy bracts and pollen used as pollinator rewards. A synapomorphy distinguishing Pandanaceae, is tristichous phyllotaxis, which imparts a radial symmetry. Of importance to the pollination biology of *Pandanus*, this phyllotactic pattern positions the bracts in three ranks beneath the inflorescence. Wind tunnel experiments on *Pandanus* showed such tristichy of the bracts to impart aerodynamic characteristics necessary for pollen capture by the pistillate inflorescence (Cox, 1985). Although highly functional, this feature cannot be considered adaptive in the strict sense since pistillate inflorescences of vertebrate-pollinated *Freycinetia reinecke* also produce similar flow patterns when placed in a wind tunnel. Given the cladogram here derived, tristichous phyllotaxis appears as a preadaptation to anemophily that was possessed by some of the ancestral pandans, and proved functional only after changes in the staminate inflorescence, such as lengthening of the internode, allowed pollen to be wind-dispersed.

It is of interest that a synapomorphy characterizing *Sararanga* and *Pandanus* is relatively elongated internode length in the staminate inflorescence. This results in a pendulous inflorescence that facilitates dispersion of pollen on the wind. As shown by the wind tunnel experiments with *Freycinetia*, the ancestral tristichy of the family made the involucrate pandanaceous inflorescence ready to function as an aerodynamically efficient pollen receiver. Thus, merely lengthening the staminate inflorescence internode made a jump from vertebrate pollination to wind pollination suddenly possible. With the advent of wind pollination, production of pollinator rewards became unnecessary. Here the change of fleshy bracts to chartaceous bracts appears as an autapomorphy characterizing *Pandanus*.

A possible autapomorphy characterizing *Freycinetia* is a lipid-rich *pollenkitt* that holds pollen to the feathers of birds and to the facial hairs of flying foxes as well as providing a pollinator reward

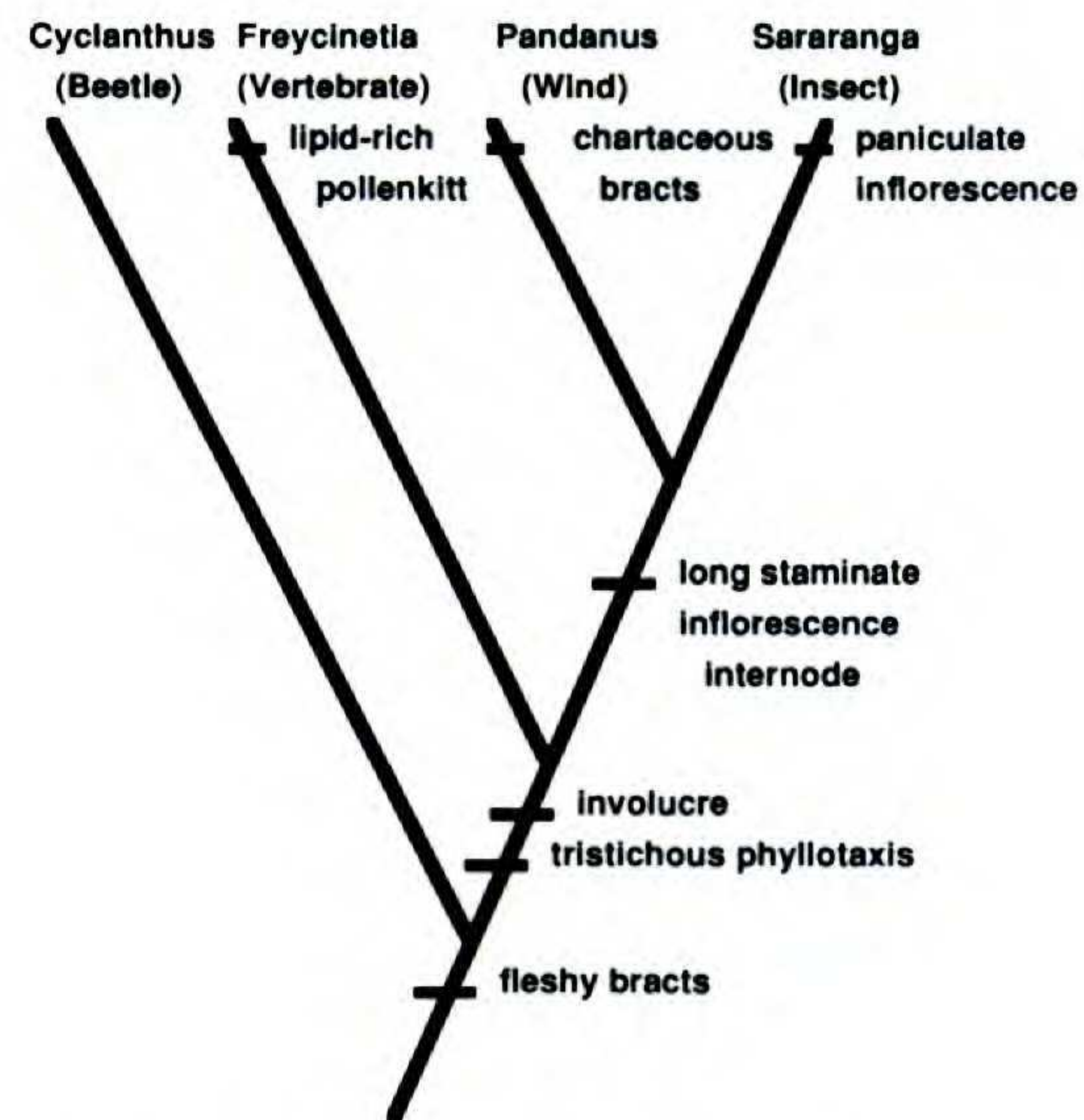


FIGURE 19. Consensus tree of pollination syndromes in Pandanaceae with *Cyclanthus* (Cyclanthaceae) used to determine polarities.

(Cox, 1984). A *pollenkitt*, however, also occurs in *Pandanus* (in *P. beccarii* and perhaps other species of sect. *Maysops*).

The characteristics of vertebrate-pollinated pandanaceous inflorescences, as revealed by extant *Freycinetia* species, make them unlikely to be pollinated by insects. For example, the open involucre cause the head of a large vertebrate pollinator, such as a bird or flying fox, to come into direct contact with the spikes as they feed on the bracts. Contact with the spikes would not be made, however, by small insects feeding on the bracts, given the distance between the attractive bracts and the spikes. Thus, even though pollen could be deposited on insects that fed on the staminate spikes, this pollen would not be transferred effectively to pistillate spikes, given the lack of nectar or other pollinator rewards offered by the pistillate spikes themselves. A reduction in size of the inflorescence resulting in closer spatial proximity of the pollinator reward to the stigmatic surfaces would be necessary for insect pollination to occur.

Something similar appears to have occurred in *Sararanga*, pending, of course, accurate determination of the morphological identity of the terminal floral units. The inflorescence is paniculate and massive, creating a large display for potential insect pollinators. The basal hexose-rich cupule or bract is positioned on the pedunculate terminal floral unit so that the body of any insect feeding on it would come in contact with the sessile stigmas. The cupule or bract of the staminate terminal floral units is in a similar position, and would thus deposit pollen in a similar manner on the body of any insect feeding on the bract.

Thus, if the Cyclanthaceae indeed proved to be the sister group to the Pandanaceae, an evolution-

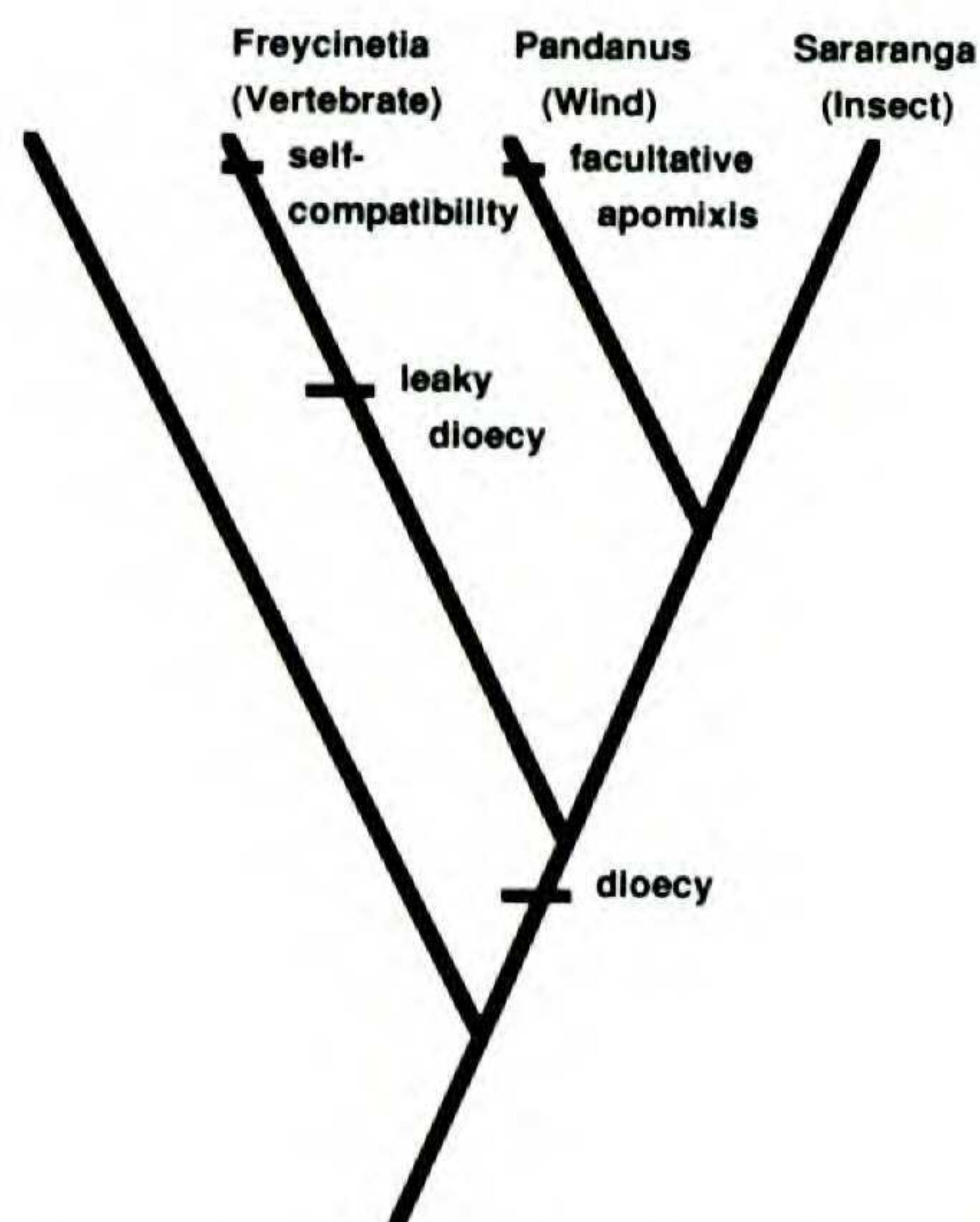


FIGURE 20. Consensus tree of Pandanaceae with primary breeding systems superimposed; polarities determined as in Figure 5.

ary sequence from vertebrate pollination to a branching point between wind pollination and insect pollination could be envisioned.

In terms of breeding system evolution, *Cyclanthus bipartitus* is monoecious, with unisexual flowers produced in alternating cycles on the congested spadix. Because, as shown in extant hermaphroditic *Freycinetia* inflorescences (Cox, 1982), vertebrate pollinators feeding on pollen cause significant damage to gynoecial structures, the advent of vertebrate pollination would cause a monomorphic (hermaphroditic) population to become vulnerable to invasion by dimorphic (dioecious) mutants (Cox, 1982, 1986). Thus dioecism, which is a synapomorphy uniting Pandanaceae (Fig. 20), may have evolved in the family in response to ancestral vertebrate pollination. Similarly, vertebrate pollination maintains dioecism in *Freycinetia* populations today (Cox, 1982). Dioecism, however, greatly reduces colonization ability (Baker & Cox, 1984). Thus, the evolution of facultative apomixis in *Pandanus* increased its ability to colonize new habitats and islands, resulting in a dramatic range extension. Dioecism may be maladaptive in relation to colonization potential in *Sararanga* because it reduces likelihood of successful pollination, and thus may partially account for its inability to colonize oceanic islands successively.

The relationships between breeding systems, pollination syndromes, ranges, and numbers of species may be highly significant in the Pandanaceae. For example, the genus *Pandanus*, with wind pollination, facultative apomixis, and water- or animal-dispersed syncarps, has the broadest range and greatest number of species. *Pandanus*, with its anemophilous pollination system, can colonize any

appropriate island regardless of the island's faunal composition. Since *Pandanus* is facultatively apomictic, successful colonization does not require the establishment of both sexes. Thus a single female propagule may eventually fill an entire island with its apomictic progeny. Through founder effect and genetic drift alone, such facultative apomixis in a plant colonizing disparate islands would be expected to result in a huge range and a massive number of species. Indeed this breeding system may partially explain some of the controversies in *Pandanus* taxonomy. For example, Stone (1976a, 1982c) and Fosberg (1977) have frequently disagreed with St. John (1979a, b) on the identity of *Pandanus tectorius*. Fosberg, for example, reduced six binomials erected by St. John from Aldabran specimens to synonymy with *Pandanus tectorius*, and Stone reduced 15 *Pandanus* species erected by St. John from coastal Australian collections to synonymy with *P. tectorius*. As Stone (1982c, p. 135) perceptively suggested, "The obvious taxonomic difficulties in certain species-groups of *Pandanus* such as the '*P. tectorius*' group and also in *Pandanus* section *Austrokeura* Stone, may be caused by apomixis."

Facultative apomixis and anemophily may also permit *Pandanus* species to colonize new habitats that would otherwise be unavailable to it if it were linked to a specific type or class of animal pollinators. Thus, allopatric speciation processes as well as genetic drift may have contributed to the high speciation rate in *Pandanus*.

Freycinetia species, on the other hand, lack facultative apomixis and water dispersal. However, their attractiveness to a wide variety of vertebrate pollinators and dispersers, as well as infrequent "leaky dioecy" (Baker & Cox, 1984), would assure them a large range and high speciation rate, albeit lower than *Pandanus*, where the apomixis coupled with abiotic dispersal has likely resulted in speciation through genetic drift.

Conversely, *Sararanga* lacks facultative apomixis, "leaky dioecy," and is apparently tied to a single class of pollinators of possibly a limited range, which may explain its small range and low number of species. Its distribution along the edge of the Tethys geosyncline and its absence from oceanic islands suggest that the distribution of *Sararanga* may be entirely due to vicariance processes, i.e., local differentiation resulting in two species.

In conclusion, recognition of the phylogenetic relationships of Pandanaceae can help in the formulation of various hypotheses concerning breeding system evolution, evolution of different pollination syndromes, and their effect on range

extension and speciation rates. In this light, Pandanaceae do not appear to be primarily anemophilous and diclinous, as Meeuse (1972) suggested, but rather they spring from vertebrate-pollinated ancestors that developed dioecism in response to destructive pollinators. Subsequently, there have been interactive effects between pollination, breeding system evolution, speciosity, and range extension, with only a few changes in inflorescence morphology, leading to the evolution of strikingly different pollination syndromes. Obviously this view is limited by the accuracy and resolution of the proposed phylogeny. It is hoped that continued interest in tropical monocotyledons will one day yield persuasive evidence for a sister group to the Pandanaceae. Such a discovery would facilitate rigorous testing of the hypotheses proposed here.

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